PLANT ECOLOGY OF THE BULLI DISTRICT.

PART II: PLANT COMMUNITIES OF THE PLATEAU AND SCARP.

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(Plates i–ii; one Text-figure.)

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Foreword.

Unavoidably, a considerable period has elapsed between the appearance of Part i of this series (Davis, 1936) and the completion, for publication, of the remaining parts. During the interval, several important papers have appeared, dealing with the plant ecology of the New South Wales coastal region (Pidgeon, 1937, 1938; Fraser and Vickery, 1937, 1938, 1939; Osborn and Robertson, 1939). With reference to the classification of the *Eucalyptus* forest communities submitted in Part i, some further clarification is now necessary.

Pidgeon (1937) has advanced a classification of the *Eucalyptus* forests of the central coastal area of New South Wales, recognizing six associations in the entire region, with subordinate consociations, and giving much broader limits to the association unit than those adopted in Part i of this series. While it is freely admitted that this broader limitation for the association is in accordance with the application of North American workers, and that certain of the 'associations' listed in Part i of this series will in time take their place as 'consociations' within broad association limits, it is submitted that insufficient is known of the environmental, genetic and phylogenetic relations of the various *Eucalyptus* forest communities safely to dogmatize on the natural grouping of consociations at the present stage. If the association be regarded as generic, and the consociation as specific, the procedure adopted in Part i represents the erection of a number of monotypic genera, whereby, admittedly, natural relationships cannot be indicated; the alternative procedure, however, runs the risk of erecting genera including unrelated species.

The following table sets out the differences in the two classifications:

Situation of Community.	*Classification of Part i.*	*Classification of Pidgeon (1937).*
Hawkesbury Sandstone, little or no physiographic shelter.	*Eucalyptus Sieberiana* Association.	Mixed *Eucalyptus* Forest Association.
Do., moderate physiographic shelter.	*E. piperita* Association.	Do.
Do., good physiographic shelter.	*E. pilularis* Association.	Do.
Narrabeen Sandstone, little or no physiographic shelter.	*E. piperita* Association.	Do.
Do., moderate physiographic shelter; Chocolate Shale, little or no physiographic shelter.	*E. saligna* Association; *E. pilularis* Association (upper coastal slopes).	? *E. saligna-E. pilularis* Association.

* *Note added 23rd September, 1940.*—An important paper on plant succession by Pidgeon (Proc. Linn. Soc. N.S.W., lxv, 221-249; issued 16th September, 1940) deals with the general aspects of the area of which the Bulli district forms merely a unit. Circumstances forbid the modification of the present two papers (Plant Ecology of the Bulli District. ii and iii) in the light of knowledge therein presented, or any discussion of points raised. Nevertheless, although much of the ground has been covered, it is still considered worth while to present these two papers in their original form, both as independent (though local and less complete) evidence of certain facts and as maintaining a somewhat different viewpoint on controversial issues.

Situation of Community.	*Classification of Part i.*	*Classification of Pidgeon (1937).*
Wianamatta Shale, little or no physiographic shelter.	*E. piperita - Angophora lanceolata* Association.	Mixed *Eucalyptus* Forest Association.
Upper Coal Measures (shales and sandstones), little or no physiographic shelter.	*E. pilularis* Association.	*E saligna-E. pilularis* Association.
Upper Coal Measures (tuffaceous mudstone), little or no physiographic shelter.	Mixed *Eucalyptus* Forest. (*a*).	Mixed *Eucalyptus* Forest Association.
Recent Alluvial Soil, little or no physiographic shelter (climax of lagoon succession).	Mixed *Eucalyptus* Forest. (*b*).	Do.

The separation, in Part i, of the '*Eucalyptus piperita-Angophora lanceolata* Association' from the normal *E. piperita* Association is not justified, and the former is henceforth referred to as the *Angophora lanceolata* facies of the *Eucalyptus piperita* Association.

Pidgeon's grouping of the *Eucalyptus saligna* and *E. pilularis* communities as a single association is probably justified. In Part i the relationship was marked by referring to the communities as corresponding associations (p. 295). The tendency of *E. saligna* to predominate at the ecotone of the *E. pilularis* Association and the rain forest formation on the coastal slopes suggests that it requires better environmental conditions than *E. pilularis.* The distinction of the two associations is tentatively retained in this and subsequent parts for uniformity with the smaller sense of 'association' used throughout.

Pidgeon's separation of the *Eucalyptus pilularis* Community into two associations depending on soil origin (on Hawkesbury Sandstone, Mixed *Eucalyptus* Forest Association, pars; on richer soils, consociation of *E. saligna-E. pilularis* Association) seems to add to the complexity of the classification. The community on Hawkesbury Sandstone is closely similar to its manifestations elsewhere, both in the form and height of the dominant tree, and also in the presence of certain species of the lower strata (e.g., *Casuarina torulosa, Leucopogon lanceolatus, Pteridium aquilinum, Imperata cylindrica* var. *koenigii, Hardenbergia monophylla*) which are characteristic of the *E. pilularis* Community on Upper Coal Measures soils, but absent from poorer sandstone soils, such as in the *E. Sieberiana* Association. Even the soil properties are similar, due to the improvement of the water-retaining capacity of sandstone soils carrying *E. pilularis*, by humus accumulation, up to a point comparable with that of soils derived from less coarsely-grained rocks.

The *Eucalyptus Sieberiana* Association is a widespread and important unit, which scarcely appears in its typical form north of the Bulli district. It is extensively developed on soils derived from Devonian sandstones on the far south coast of New South Wales, particularly in the Eden district. It also occurs in Victoria and Tasmania, where it assumes the appearance of a wet sclerophyll forest, regarded by some workers as a distinct formation or sub-formation (Wood, 1937), although the distinction is arbitrary. North of the Bulli district other species (e.g., *E. gummifera, E. haemastoma*) occupy more important places on correspondingly poor soils, although *E. Sieberiana* extends north as far as the Hawkesbury River.

The separation of the communities dominated by *Eucalyptus piperita* from the *E. Sieberiana* Association appears to be justified, in order to emphasize the fact that *E. piperita* represents a definite grade higher than *E. Sieberiana* in soil requirements, just as *E. pilularis* represents a grade above *E. piperita.* This gradation tends to be obscured by grouping together under the one unit, as the Mixed *Eucalyptus* Forest Association of Pidgeon. It could be equally emphasized by calling the grades consociations (as allowed by Pidgeon, 1937, p. 335), but it would be difficult to group three such consociations into an association without harming other parts of the classification system, e.g., the recognition of the *E. pilularis* unit on all soil types, discussed above.

The classification of Part i is therefore retained throughout the series, with the exception of the *E. piperita-Angophora lanceolata* Association noted above. The classification has sufficient utility for the limited district here dealt with, although it would be difficult to apply it, even with logical extensions, throughout the entire sclerophyll formation of eastern Australia. This difficulty need not be met in the present series, which is purely local in nature; it is hoped that some synthesis of the different classifications will develop when the entire formation comes to be considered. It is further emphasized that the divergence from the classification of Pidgeon does not indicate a divergence in the observance of facts, but merely in opinion as to convenience of tabulation.

Nomenclature.

In general, the same procedure in taxonomic names is followed as in Part i, authors' names being appended to species only where the names given by Moore and Betche (1893) are not adhered to. For Pteridophytes the names given by Melvaine (1936) are used throughout, without authors. Many of the names used by Moore and Betche have now been superseded, but this work is nevertheless the only flora available to field workers. In a few cases the names used in Part i have been changed in this and subsequent parts for uniformity with the ecological papers mentioned above. The following are the changes:

Eucalyptus gummifera (Gaertn.) Hochr. (*E. corymbosa* of Part i); *Imperata cylindrica* Stapf. var. *koenigii* D. & S. (*I. arundinacea* of Part i); the generic name *Lomandra* is henceforth used in place of *Xerotes*. The name *Gymnoschoenus sphaerocephalus* (R.Br.) Hook. f., as used in Part i, is retained; this is apparently the correct name (see, e.g., Black, 1929, p. 91), although the species is listed by Moore and Betche as *Schoenus sphaerocephalus* Poir. (syn. *Mesomelaena sphaerocephala* Benth.), and by the Census (Maiden and Betche, 1916) as *Gymnoschoenus adustus* Nees.

METHODS.

(i). *Soil Analyses.*—A large number of soil samples were tested for various properties, and since the methods used, though constant throughout, were not the usual standard methods, they are detailed fully. The figures are strictly comparable *inter se*, but not necessarily with those given by other workers.

Except for pH and water content, all samples were passed through a sieve with circular holes of diameter 1 mm. The pH was determined by the quinhydrone method (gold electrode), standard procedure being adopted to eliminate the vitiation of the results for comparative purposes by drift. Soils were stirred with distilled water and quinhydrone, stood for 45 minutes, and again stirred. At the end of a further 15 minutes the E.M.F. was read without further stirring.

To estimate comparative water content the soils from a series were collected at the same time in sealed jars, and samples weighed as soon as possible. These were then dried at 90–100°C., the water content being calculated as a percentage of the dry weight.

The method of determining water-retaining capacity gives a higher reading than the methods usually adopted. Metal cylinders (height 2·5 cm.; diameter 5 cm.) with gauze bottoms were lined with filter-paper, cut to cover the bottom but to allow drainage at the periphery, since drainage through the filter-paper becomes impeded by clay particles. The lined cylinders were weighed dry (m_1) and wet (m_2). They were then filled with saturated soil, drained for 30 minutes, and weighed (m_3). The whole was then dried to constant weight (m_4) at 90–100°C. The water-retaining capacity is calculated thus: $\frac{m_3-m_4-(m_2-m_1)}{m_4-m_1} . 100$, representing a percentage of the dry weight. The usual method of weighing soil dry, and allowing it to take up water, proved impracticable, as dry soils, especially sandy soils with high organic content, could not be caused to take up water without loss of part of the sample from the container. The high temperature of drying (90–100°C.) in the method used was essential from considerations of time; but it renders the final figure for water-retaining capacity high by including in it some water not available to plant roots.

Loss on ignition, of soils previously dried at 110°C., expressed as a percentage of the dry weight, gives a reasonably close approximation to the total organic content (humified and unhumified). Exceptions are soils of high clay content (especially Wianamatta Shale soils, and to a less extent soils from Chocolate Shale and some of the Upper Coal Measures), and the early stages of the sand-dune succession described in Part iii, where a fair proportion of calcium carbonate is present.

In representative samples the portion of the figures for loss on ignition, represented by humus, was estimated by determining the percentage of the original soil decomposed to gaseous and volatile substances by continued treatment with hot 6% hydrogen peroxide.

The chloride contents (listed in Part iii) were obtained by lixiviating a known weight of oven-dry soil with distilled water, and estimating the filtrate with standard silver nitrate. The chloride contents are expressed as a percentage weight of chlorine (chloride ion) per dry weight of soil. This figure is undoubtedly variable for any situation, due to seasonal factors of spray incidence and leaching. All the figures given refer to soils collected in July 1938, a period preceded by some time of low rainfall and little leaching. Figures for salinity of soil solution, as sodium chloride, grm. per litre (Lagatu and Sicard, 1911), depending on the water-content of the soil, may be calculated from the data of Table 4, Part iii. This factor, although it is at any one time a truer index of the conditions to which plant roots are subjected, must be exceedingly variable for any situation, due to seasonally varying soil moisture.

For all the above factors, soils of the A_1 horizon (1–4 inches), the zone of maximum utilization by plant roots, have been determined.

Percentage of water held at sticky-point and sand fraction were estimated for soils of varying origin. From these results the index of texture (Hardy, 1928) was calculated (percentage of water held at sticky-point less one-fifth percentage of sand). The samples used for this work were from the A_2 horizon, as in the A_1 horizon varying organic content would affect the water held at sticky-point; whereas the property, the investigation of which is here desired, is that of the original soil as conditioned by parent rock, and not the soil resulting from the interaction of vegetation with original soil.

The index of texture actually appears to be a less useful index of the soil with respect to vegetation than is the percentage of water held at sticky-point alone. The index of texture suffers further in that no distinction is made in its calculation between coarse and fine sand, both lowering the index of texture figure equally. Thus almost all the sand fraction of Hawkesbury Sandstone soils is coarse sand, and almost all that of Chocolate Shale soils is fine sand, the latter with a greater capacity to hold water in the estimation at sticky-point.

(ii). *Floristics.*—Only in the relatively homogeneous *Gymnoschoenus sphaerocephalus* Community (swamp subclimax on Hawkesbury Sandstone) were accurate quadrats undertaken. These took the form of metre-quadrats, each shoot of the rhizomatous vegetation being removed by shears and counted as one unit. This procedure was necessitated by the density of the vegetation (Pl. ii, C).

In the lower strata of the remaining communities, and in the tree stratum of the brush or rain-forest, rough counts of the numbers of each species in a series of areas were made. These areas were circles of 10 yard radius or, for brush trees, 20 yard radius. For each community, the number of individuals of each species was multiplied by the factor necessary to bring the commonest species to 100 units. The species were then graded into five classes: abundant (A), 100–41; common (C), 40–16; occasional (O), 15–6; rare (R), 5–3; and very rare (VR), 2 or less. These limits were chosen in consideration of the lack of complete domination by one species of the strata examined; it is clear that a species occurring in a ratio of 1:25 to the commonest species would not be rare, in the accepted sense, if the commonest species practically dominated the community; but in the communities examined co-dominance of a number of species was the rule.

Some modification of the results obtained was found necessary, due to the accumulation of additional data by inspection, without analysis, of certain areas not visited when the counts were made. This applies especially to the Hawkesbury Sandstone shrubs. The classes are therefore only approximate, but probably closer to the truth than a gradation by inspection alone could attain.

The proportion of the counts in which each species appeared gave some indication as to localization, and in the floristic lists species are tabulated as local (L) if this feature is particularly marked.

Plant Communities of the Plateau and Scarp.

(1) *Hawkesbury Sandstone.*

(*a*). Eucalyptus Sieberiana *Association.*

This community (Pl. i, A and B), present in situations on the Hawkesbury Sandstone lacking physiographic shelter, is usually associated with fairly efficient drainage conditions, although the dominant occasionally approaches positions of fairly high water-table near the ecotone with swamp communities. Soils are typically of a depth greater than three feet, often much more, but in some places the association occurs on shallower soils, the dominant then being dwarfed and often malformed. These areas may be regarded as a stage in the lithosere, detailed later, immediately preceding the true climax.

Soil properties for certain typical parts of the association are given in Table 1. The texture of the soil originating from Hawkesbury Sandstone is coarse, although the weathering of local shale bands in this series gives a small but definite clay fraction in some places, and in particular gives the B horizon in most places the nature of a clay-sand. The following estimates were obtained for A_2 soils:

Water held at sticky-point 22–29%; sand fraction 96–97%; index of texture 3–10.

The uniformly low organic content is insufficient to counteract the coarseness of the soil, and the water-retaining capacity is low. The highest figure for water-retaining capacity (37%) represents a sample with higher clay-content than normal. Of the figures given for loss on ignition (2·3–3·5%), some 50% appears to represent humus. The soils are markedly acid, and appear to be poor in nutrient elements.

TABLE 1.
Properties of Soils on Hawkesbury Sandstone carrying Climax and Post-climax Communities.

——	W.R.C. (%).	Loss on Ignition (%).	pH.
Eucalyptus Sieberiana Association	25	2·5	5·4
	29	3·2	4·9
	28	3·0	4·9
	29	2·9	5·2
	37	2·3	4·5
	33	3·5	4·9
Eucalyptus piperita Association..	43	7·3	5·2
	46	8·0	4·4
	49	8·7	4·6
	78	26·0	4·9
	83	30·0	4·7
	76	23·0	5·1
Eucalyptus pilularis Association	80	23·0	5·0
	91	33·0	5·0
Eucalyptus piperita Association, near Brush Ecotone (Loddon Falls)	113	49·0	4·6
Brush	90	30·0	5·2
	120	35·0	5·2
	120	49·0	5·3
	130	48·0	5·0

Some indication of the range of the dominant has been given earlier. A consideration of its environment elsewhere suggests that neither poor drainage nor shallowness of soil is one of the limiting factors here preventing the development of species such as *Eucalyptus piperita* and *E. pilularis*. These factors are rather to be sought in the coarseness of the soil texture, and the resulting low water-retaining capacity in the absence of humus development.

Structurally the association is composed of a tree stratum typically 40–60 feet high, with discontinuous canopy. Low trees are relatively unimportant, *Banksia serrata* being common only in limited areas; some of the larger shrubs, however, fall within the microphanerophyte class. The shrub stratum is prominent and floristically diverse, though usually not continuous. The ground stratum seldom forms a complete cover, except in areas tending towards swamp conditions. The classification into life-forms is indicated in the floristic lists.

Floristically, the composition of the association is as follows:

MM:* A, *Eucalyptus Sieberiana* (dominant); O(LC), *E. gummifera*, *E. micrantha* Benth.; VR(L), *Casuarina suberosa*, *Acacia elata*.

M: LC, *Banksia serrata* (Shrubs); C, *Leptospermum stellatum*, *L. flavescens*, *Banksia ericifolia*; O, *Hakea acicularis*; VR(L), *Kunzea corifolia*.

N: A, *Grevillea oleoides*, *Hakea dactyloides*, *H. pugioniformis*, *Isopogon anemonifolius*, *Lambertia formosa*, *Persoonia lanceolata*, *P. salicina*, *Petrophila pulchella*, *Leptomeria acida*, *Olax stricta*, *Acacia discolor*, *A. juniperina*, *A. suaveolens*, *Aotus villosa*, *Bossiaea heterophylla*, *B. scolopendria*, *Dillwynia floribunda*, *Pultenaea elliptica*, *Ricinocarpus pinifolius*, *Pimelea linifolia*, *Leptospermum scoparium*, *Epacris microphylla*, *E. obtusifolia*, *Leucopogon juniperinus*, *L. microphyllus*, *Sprengelia incarnata*, *Dampiera stricta*; C, *Banksia spinulosa*, *Conospermum ellipticum*, *C. taxifolium*, *Grevillea sericea*, *G. punicea*, *Lomatia silaifolia*, *Acacia myrtifolia*, *Gompholobium latifolium*, *Comesperma ericinum*, *Baeckea crenulata*, *B. linifolia*, *Kunzea capitata*, *Trachymene linearis*, *Epacris paludosa*; O, *Symphonema paludosum*, *Xylomelum pyriforme*, *Daviesia ulicina*, *Gompholobium grandiflorum*, *Eriostemon Crowei*, *Phebalium diosmeum* Juss., *Dodonaea triquetra*, *Stackhousia viminea*, *Callistemon lanceolatus*, *Calythrix tetragona*, *Darwinia virgata*, *Leucopogon collinus*, *Woolsia pungens*, *Hemigenia purpurea*; R, *Banksia paludosa* R.Br., *Telopea speciosissima*, *Phyllota phylicoides*, *Boronia pinnata*, *Lasiopetalum ferrugineum*, *Epacris longiflora*, *Leucopogon virgatus*, *Chloanthes Stoechadis*; VR, *Banksia aemula*, *Grevillea sphacelata*, *Cryptandra ericifolia*, *Melaleuca squamea*, *Leucopogon amplexicaulis*, *L. esquamatus*, *Dampiera Brownii*.

Ch: A, *Lomandra obliqua* MacBride, *Patersonia glauca*; C, *Doryanthes excelsa*, *Mirbelia reticulata*, *Tetratheca ericifolia*, *Ampera spartioides*, *Hibbertia stricta*, *Stylidium graminifolium* Swartz; O, *Xanthorrhoea hastilis*, *Patersonia sericea*, *Conospermum tenuifolium*, *Grevillea capitellata*, *Darwinia taxifolia*, *Xanthosia pilosa*, *Opercularia ovata*, *Pomax umbellata*, *Lobelia dentata*; R, *Gompholobium minus*, *Hovea heterophylla*, *Hybanthus filiformis*, *Viola hederacea*, *Styphelia triflora*, *Goodenia heterophylla*; VR, *Kennedya prostrata*, *Comesperma volubile*.

H: A, *Haemodorum planifolium*, *Actinotus minor*; LC, *Selaginella uliginosa*; O, *Gahnia psittacorum*, *Lomandra longifolia* Labill., *L. filiformis* J. Britten; R, *Eragrostis Brownii*, *Stipa pubescens*, *Caustis flexuosa*, *Tricostularia paludosa* Benth., *Haemodorum teretifolium*; VR, *Entolasia marginata* Hughes, *Caustis pentandra*, *Stypandra caespitosa*, *Rubus fruticosus* (introd.).

G: A, *Leptocarpus tenax*, *Lepyrodia scariosa*; O, *Thelymitra ixioides*; VR, *Burchardia umbellata*, *Cryptostylis longifolia*, *Glossodia major*.

E: O, *Cassytha paniculata*, *C. pubescens*;† VR, *Loranthus celastroides*.‡

The above lists include some species (e.g., *Symphyonema paludosum*, *Olax stricta*, *Baeckea* spp.) which are more characteristic of swampy areas, and others (e.g., *Leptocarpus tenax*, *Lepyrodia scariosa*) which occur in this association and in swamps in approximately equal frequencies. The frequency given above in all cases represents

* Abbreviations for life-forms, frequency, and localization used throughout paper: MM, mega- and mesophanerophytes; M, microphanerophytes; N, nanophanerophytes; Ch, chamaephytes; H, hemicryptophytes; G, geophytes; HH, helo- and hydrophytes; S, stem-succulents; E, epiphytes. (Actually, no hydrophytes are present in the species listed under HH.) A, abundant; C, common; O, occasional; R, rare; VR, very rare; L, local or locally; LC, locally common (see METHODS, *Floristics*).

† Rooted hemiparasites, classed as "E", the nearest life-form.

‡ In these lists the species are arranged in order of families according to the classification of Engler and Prantl, and within each family, alphabetical.

that observed in the *Eucalyptus Sieberiana* Association, regardless of the frequency of the species elsewhere; it has been noted earlier that this association extends in some cases to rather poorly-drained soils.

Apart from minor environmental variations, such as in efficiency of drainage, with their resultant influences, e.g., on the proportion of swamp-tolerant species, the association is characterized by local variations, often striking, without apparent environmental cause. These variations are most marked in the shrub stratum; they may well be due to chance occurrences in seed dispersal, and to the extinction of some species in belts where bush-fires of preceding years have been most severe.

Two environmental variants were noted in Part i:

(1). On the eastern edge of the plateau, particularly north of Sublime Point, on the gradual slope running down towards the sandstone scarp (Fig. 1), the vegetation assumes an aspect slightly different from other parts of the plateau. Drainage conditions are good, so that species favoured by swampy conditions are absent. *Eucalyptus gummifera* increases in abundance, often becoming nearly as important as *E. Sieberiana*; both species are frequently stunted, as the soil is often very shallow. In most places the cover by the lower strata increases, often to 100%. Additional species found in this zone, but not elsewhere in the association, include:

N: *Xanthorrhoea arborea* R.Br., *Hakea saligna, Persoonia revoluta, Pultenaea daphnoides, Correa speciosa, Actinotus Helianthi, Dracophyllum secundum, Cassinia denticulata, Olearia elliptica* DC.

N (climbers): *Smilax glycyphylla, Billardiera scandens.*

Ch: *Dianella coerulea, Halorrhagis teucrioides, Helichrysum scorpioides.*

G: *Lycopodium densum, Gleichenia flabellata.*

Certain species found elsewhere in the association increase in prominence; the following may be specified:

N: *Banksia spinulosa, Boronia pinnata, Phebalium diosmeum* Juss., *Lasiopetalum ferrugineum, Epacris longiflora, Chloanthes Stoechadis.*

Ch: *Xanthosia pilosa, Opercularia ovata.*

The factor inducing this variation seems to be the shelter from the west, which, while too slight to affect the trees, allows certain more mesophytic types to develop in the lower strata. The soil differs little, if at all, from that in other parts of the association. Certain species cannot be considered more mesophytic than those of other areas; such forms as *Xanthorrhoea arborea* and *Actinotus Helianthi*, occurring only at the very edge of the plateau, are to be considered rather as species limited to very dry, rocky habitats.

(2). The slopes facing west, in the more westerly parts of the area studied, are characterized by better drainage and lower rainfall than the flatter areas of the eastern parts of the plateau (cf. Part i). *Eucalyptus gummifera* increases in relative abundance; in the lower strata there are a decrease in percentage cover and a general absence of swamp-tolerant species.*

The *Eucalyptus Sieberiana* Association is in general similar to much of the low forest on sandstone in the Sydney district, although its dominant fails to reach such development near Sydney either in size or frequency. The lower strata are somewhat poorer floristically than in corresponding situations near Sydney, and possess very few additional species (e.g., *Grevillea oleoides*).

(*b*). *Developments subject to Physiographic Shelter.*

With increasing physiographic shelter, Hawkesbury Sandstone soils carry successively higher types of vegetation, the sequence being *Eucalyptus piperita* Association-*E. pilularis* Association-Brush (sub-tropical rain-forest) (Pl. i, C, D, E respectively). The characteristics of the soils of this series are listed in Tables 1 and 2. The series is characterized by a successive rise in organic content of the soil, proportionally raising the water-retaining capacity, which appears to be the chief factor influencing the development of the first two associations. The addition of a higher

* The occurrence of some well-developed trees of *Syncarpia laurifolia* Ten. near the Bulli Lookout, intermingled with *E. Sieberiana* in an otherwise normal part of the association, is absolutely unexplained. *Syncarpia* is a unit of a much higher vegetational community.

TABLE 2.

Hawkesbury Sandstone Soils on Transect with Increasing Shelter.

——	W.R.C. (%).	Loss on Ignition (%).	pH.	Water Content (%) (10.7.38).
Eucalyptus Sieberiana Association ..	37	2·3	4·5	1·9
E. piperita Association	46	8·0	4·4	8·2
E. pilularis Association	80	23·0	5·0	12·9

proportion of humus* to a soil of coarse texture raises the water-retaining capacity to the level of finer soils with less humus, such as carry these associations on the other geological series of the district.

The rise in organic content seems to be associated chiefly with a high average moisture-content, a result of drainage conditions and weak insolation, depending on the physiography. It is not comparable with the rise of organic content under swampy conditions, to which are limited plants tolerant to low pH and poor root aeration. Apart from moisture-content, other factors inducing a high organic content in this series are decreased insolation and infrequency of bush-fires, both factors directly combating oxidation of soil humus. The infrequency of bush-fires is dependent on the relatively moist nature of the habitat and vegetation.

In no case studied could the full vegetational sequence be observed on a single transect. In the more gradual valleys south of Cataract Reservoir, *Eucalyptus Sieberiana* gives place to *E. piperita* (on the upper slopes) and *E. pilularis* (on the lower slopes and valley floor); shelter is throughout insufficient for brush, which however develops where erosion has led to the penetration of the Narrabeen beds at the bottom of some gullies. In the abrupt Hawkesbury Sandstone gorge at Loddon Falls, brush is developed at the lower levels; on the steep sides, *Eucalyptus piperita* occurs. *E. pilularis* does not

* Humus accounts for approximately half of the loss-on-ignition figures of Tables 1 and 2.

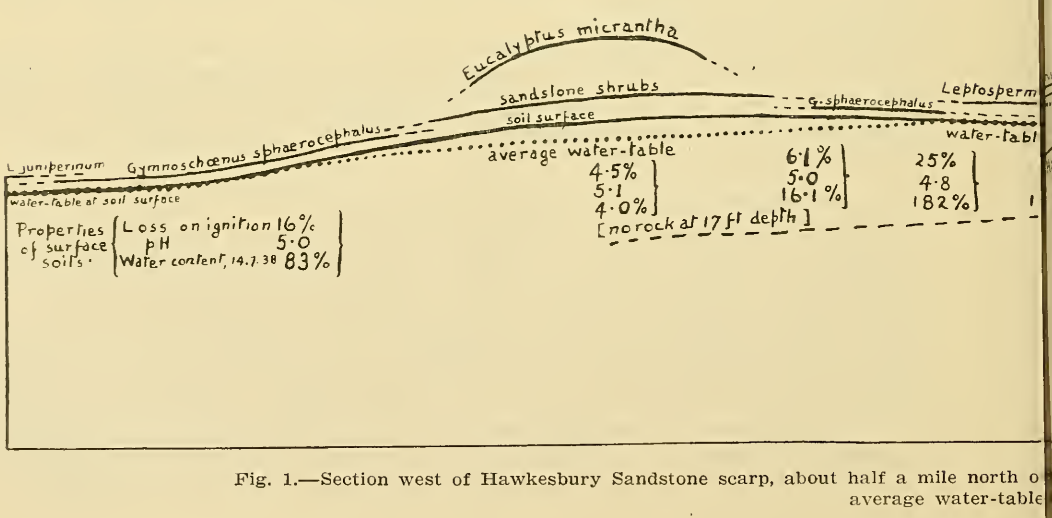


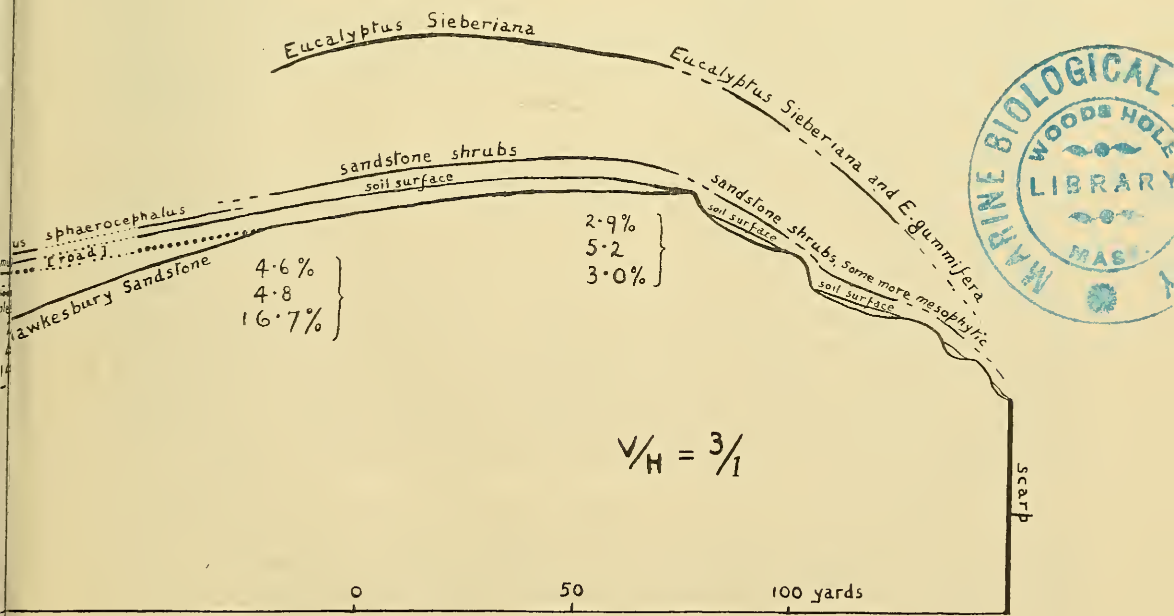
Fig. 1.—Section west of Hawkesbury Sandstone scarp, about half a mile north o
average water-table

develop, the ecotone between the *Eucalyptus piperita* Association and the brush formation, where soil conditions are suitable for *E. pilularis*, is very narrow, due to the steepness of the slope. Brush is developed to a limited extent in several ravines in the Hawkesbury Sandstone scarp at the eastern limit of the plateau; *Eucalyptus piperita* and *E. pilularis* do not develop here as intermediates, the belt between *E. Sieberiana* (on the edge of the plateau) and the brush (in the floor of the ravine) constituting the rocky shoulders of the ravine, almost devoid of soil.

The limitation of brush to the lower parts of the Loddon Falls gorge and to the scarp ravines, together with a general consideration of brush development in the Bulli district as a whole, suggests that this formation is conditioned primarily by shelter from wind and sun, secondarily only by soil requirements. The assumption that *Eucalyptus piperita* and *E. pilularis* are conditioned by soil alone, and not by wind and sun, is based on the fact that their canopies are fully exposed in most situations studied on Hawkesbury Sandstone as on other soils.

Additional elements of the *Eucalyptus piperita* and *E. pilularis* Associations on the Hawkesbury Sandstone include the mesophanerophyte, *Casuarina torulosa* (second association only), and the microphanerophytes, *Hakea saligna*, *Persoonia linearis*, *Exocarpus cupressiformis*, *Acacia longifolia*, *A. mollissima* and *Elaeocarpus reticulatus*; the nanophanerophytes, *Trachymene Billardieri* and *Leucopogon lanceolatus*; the chamaephytes, *Hibbertia Billardieri* and *Hardenbergia monophylla*, and the geophyte *Pteridium aquilinum*. These are absent from the *E. Sieberiana* Association. There are also present species found in the *E. Sieberiana* Association only at the extreme east of the plateau (e.g., *Smilax glycyphylla*, *Pultenaea daphnoides*, *Halorrhagis teucrioides* and *Cassinia denticulata*), and species of the normal *E. Sieberiana* Association (e.g., *Banksia spinulosa*, *Persoonia salicina*, *Lasiopetalum ferrugineum* and *Dodonaea triquetra*), sometimes increased in frequency compared to the *E. Sieberiana* Association (e.g., *Entolasia marginata* Hughes and *Viola hederacea*).

The high and low trees are characteristic of the *Eucalyptus piperita* and *E. pilularis* associations on other geological formations, the Eucalypts in some cases reaching nearly 100 feet in height. The lower strata include many of the same species as are found in these associations on other geological series, but are structurally different,



g height and composition of vegetation, outline of soil surface, soil properties,
tour of rock surface.

especially in the lower percentage cover. This latter is partly due to the fact that Hawkesbury Sandstone situations carrying these associations (sloping valley sides) have a fairly high percentage of exposed rock.

Brush, as developed at Loddon Falls (Pl. i, E), has a structure more or less typical of this formation on other geological series (closed canopy, absence of shrubs, presence of a ground layer of ferns), but is very poor floristically:

MM: *Doryphora Sassafras, Cryptocarya glaucescens, Callicoma serratifolia, Pittosporum undulatum, Eucryphia Moorei, Tristania laurina.*
M: *Drimys insipida* Druce, *Tristania neriifolia.*
Ch: *Todea barbara.*
H: *Adiantum diaphanum, Asplenium flabellifolium.*
E: *Davallia pyxidata, Pleopeltis diversifolia, Tmesipteris tannensis.*
(Epiphytes, also growing on rock surfaces.)

The only common tree amongst these, which is characteristically a brush type (as opposed to a member of the 'wet gully' or creek-edge flora), is *Doryphora Sassafras. Callicoma* and *Pittosporum*, though often occurring in true brush, also extend to the 'wet gully' flora, a brush-sclerophyll ecotone community, while the species of *Tristania* commonly occur beside rocky creeks, often with little shelter from wind and sun.

(*c*). *Lithoseres.*

It is impossible adequately to account for rock succession or zonation without first considering the past history and present course of the physiographic development of the area studied. The sandstone plateau, part of the Nepean Ramp, is an example of rejuvenated physiography, representing a late Tertiary peneplain raised by Pleistocene uplift.* As such, its exposed rock surfaces are mostly manifestations of a highly immature topography. To this extent, the postclimax communities detailed in the preceding section may be considered expressions of a purely allogenic succession.

On the evidence of the physiographic facts cited above, zonations between bare rock and forest, except possibly in the case of certain of the moist lithoseres detailed later, are, on the average, retrogressive, though many simulate temporal succession, and in some cases exposure of a new rock surface by physiographic change (falls of rock, or scouring of soil into a relatively recently-formed gully) may be followed by colonization and true succession up to a certain stage, that is, up to a time when denuding factors once again come into play. In spite of general retrogression, it is convenient to regard the zonation stages from rock to forest as a lithosere, whilst remembering that allogenic factors prevent true succession to a climax under the average conditions of the area. The ultimate peneplanation of the area, in the processes of which plant life undoubtedly plays a part (e.g., in rock decomposition), is too distant to visualize in terms of the present flora.

Bare rock surfaces, leading by a vegetational zonation of xeric communities to forest, are to be found at the extreme easterly edge of the plateau, and also on its more dissected parts (e.g., west of Darkes' Forest, above Cataract Reservoir, and near Loddon Falls). Where the plateau abuts on the scarp, and on the gullies of these dissected regions, it exhibits bare rock at the edge, leading back to forest by a sequence of stages of vegetation, accompanied by an increase in soil depth. The plants nearest to the bare rock surface are most frequently xeric mosses, less frequently lichens, ferns (*Polypodium Billardieri, Cyclophorus serpens*) or orchids (*Dendrobium linguiforme, D. speciosum*). Next in linear sequence comes a zone of herbs and straggling shrubs (e.g., *Tillaea Sieberiana* Schultes, *Darwinia taxifolia*), leading to a community of typical sandstone shrubs (notably *Boronia pinnata, Actinotus Helianthi*, and certain Epacridaceae), and so to *Eucalyptus* forest, the trees being frequently stunted in the zone of shallower soil.

The floristics and soil changes of this sere have been fully detailed by Pidgeon (1938, pp. 4-15), and will receive no further consideration here. The situations listed above, where the plateau gives place to the easterly scarp or to dissecting gullies, are characterized by a soil becoming more shallow as the sudden fall in surface is approached. It should be obvious that westerly migration of the scarp, or further

* Or uplift immediately preceding Pleistocene times.

dissection of the plateau by gullies (processes which are surely though gradually going on) can lead only to a decrease in size of the plateau, the communities of the plateau edge, which may be assumed to be more or less in equilibrium with the existing topography, being gradually forced backwards, whilst maintaining their present zonation. The immediate result of this process of erosion will be to denude of soil a greater percentage of rock than is exposed at present, although in some local instances conditions in newly-formed gullies will possibly be suitable for some of the postclimax communities dealt with in the preceding section.

Young trees of *Eucalyptus gummifera* have been noted on certain of the most easterly parts of the plateau, where shallow soil and bare rock form a mosaic of fairly level surface. Were it not for the westerly migration of the scarp, such a situation would almost certainly lead to the formation of the *Eucalyptus Sieberiana* Association. This development may be taking place in a few isolated cases, as the migration of the scarp is slow in terms of plant growth.

The rock exposures of the dissected areas (e.g., alternating ridges and gullies leading down to Cataract Reservoir) are more confused than those on the plateau edge, being usually represented by boulders projecting well above the soil surface. In such cases zonation is more abrupt and irregular than on the rock exposures of the more level areas of the plateau.

Zonation from rock to forest under wet, swampy conditions is characteristic of many parts of the plateau. In some cases at least, as where the rock exposure is surrounded by soil, deepening to carry forest vegetation, it seems probable that autogenic succession in time is proceeding. The succession is marked by an increase in soil depth and, in the later stages, a lowering of the water-table. Soil properties, illustrating this, and the decreasing organic content, are listed in Table 3. It should be noted that, although the water-content of the soil is here shown as successively decreasing, this does not apply under all weather conditions; in dry weather, the water-content of the soil of the first stage falls below that of the swamp stage.

TABLE 3.

Soil Properties for Moist Lithosere on Hawkesbury Sandstone.

——	W.R.C. (%).	Loss on Ignition (%).	pH.	Water Content (%) (2.7.38.)
Wet Moss Stage	73	17·0	4·9	71·0
"Hemicryptophyte Stage"	57	12·0	5·0	61·0
Local Swamp	39	5·6	5·1	47·0
Local Swamp (with shrubs)	37	4·3	5·1	35·0
Eucalyptus micrantha Stage	32	3·1	5·4	14·0
Eucalyptus Sieberiana Association (climax)	25	2·5	5·4	4·4

The earliest stage of this moist lithosere (Pl. i, G) consists of mosses (unidentified), which are followed by the 'hemicryptophyte stage' (Pidgeon, l.c.), the most prominent species of which is *Lepyrodia scariosa*; the herbs *Drosera peltata*, *D. pygmaea*, *D. spathulata*, *Mitrasacme polymorpha* and *Utricularia lateriflora* are also common. This stage leads, by deepening of the soil, to the swamp stage, of the following floristic composition:

N: A, *Banksia latifolia*, *B. latifolia* var. *minor*, *Hakea pugioniformis*, *Epacris microphylla*, *Sprengelia incarnata*; C, *Symphyonema paludosum*, *Olax stricta*, *Viminaria denudata*, *Baeckea crenulata*, *B. linifolia*, *Leptospermum juniperinum* Sm.; O, *Grevillea oleoides*, *Persoonia salicina*, *Aotus villosa*, *Dillwynia floribunda*, *Callistemon lanceolatus*, *Leptospermum lanigerum*, *Melaleuca squarrosa*, *Epacris obtusifolia*, *E. paludosa*, *Dampiera stricta*; R, *Banksia paludosa* R.Br., *Hakea dactyloides*, *Isopogon anemonifolius*, *Lambertia formosa*, *Stackhousia viminea*;

VR, *Persoonia lanceolata, Petrophila pulchella, Pultenaea elliptica, Pimelea linifolia, Melaleuca thymifolia, Trachymene linearis.*
(Note: Some of the above shrubs, e.g., *Grevillea, Isopogon, Lambertia*, do not extend to the wettest parts of the swamps; most, however, are present under all conditions. The frequencies are for the average of a variety of local swamps.)

Ch: A, *Bauera rubioides* (incl. var. *microphylla*), *Mitrasacme polymorpha*; C, *Drosera binata, D. spathulata, Euphrasia Brownii, Utricularia lateriflora, Goodenia bellidifolia*; O, *Drosera peltata, D. pygmaea, Boronia parviflora, Stylidium graminifolium* Swartz; R, *Hibbertia stricta*; VR, *Xanthorrhoea hastilis, Mitrasacme paludosa, Villarsia exaltata* F.v.M., *Utricularia dichotoma.*

H: A, *Selaginella uliginosa, Gymnoschoenus sphaerocephalus, Hypolaena lateriflora* Benth., *Xanthorrhoea minor*; C, *Lindsaya linearis, Actinotus minor*; O, *Gahnia psittacorum, Tricostularia paludosa* Benth., *Xyris gracilis, Haemodorum planifolium*; VR, *Caustis flexuosa, Juncus planifolius, Haemodorum teretifolium.*

HH: A, *Gleichenia dicarpa, Leptocarpus tenax, Lepyrodia scariosa, Restio complanatus, Chorizandra sphaerocephala, Lepidosperma laterale*; LC, *Lycopodium laterale*; O, *Blandfordia nobilis, Sowerbaea juncea*; VR, *Burchardia umbellata.*
(Note: All apparently cryptophytic species are classed as helophytes.)

Th: O, *Halorrhagis micrantha*; R, *Centrolepis strigosa.*

E: R, *Cassytha pubescens.*

The *Eucalyptus Sieberiana* Association, which may be regarded as the climax under these conditions, is reached only where drainage factors allow the lowering of the average water-table. *Eucalyptus micrantha* Benth. usually forms a definite ecotone between the swamp and the climax (Pl. i, H).

The parts of the swamp closer to the forest may be recognized as 'shrub swamp' (Pidgeon, l.c.); they are composed of the same species as are found in the swamp stage, with an increase in abundance of the shrubs found in the swamps, together with some shrubs less tolerant of a very high water-table. Even in the 'shrub-swamp', the shrub stratum is not nearly continuous; the ground stratum of both swamp and 'shrub-swamp' is continuous, the height of the vegetation being from 1–2 feet.

In one case, a young tree of *Eucalyptus micrantha* was noted in the 'shrub-swamp' stage, well beyond the limits of the older trees, indicating successional relationship in time.

(*d*). *Extensive Swamp or Moor Communities.*

On the relatively flat parts of the plateau, usually on deep soils (presumably part of the late Tertiary peneplain), extensive swamp or moor communities develop, sometimes up to 2–3 miles in extent. These swamps are particularly well developed immediately to the north and west of Sublime Point. The inhibition of tree development is due primarily to the high water-table; wherever the average water-table falls below 3–4 feet, *Eucalyptus Sieberiana*, or more often *E. micrantha* Benth., develops. This relationship is shown in Figure I, a section west of the scarp about half a mile north of Sublime Point. The soil properties of this large swamp, which may be termed the *Gymnoschoenus sphaerocephalus* Community (Pl. ii, A), are shown in Table 4. The soil is characterized by a high organic content (some 60% of the loss-on-ignition figure

TABLE 4.
Swamp Soils on Hawkesbury Sandstone.

——	W.R.C. (%).	Loss on Ignition (%).	pH.
Gymnoschoenus sphaerocephalus Community ..	81	21·0	4·8
	91	23·0	4·7
	120	25·0	4·8
Local Swamp	58	16·0	5·0
Moor at Madden's Plains	33	3·5	4·9
	39	4·2	4·8
	40	5·7	4·8
Shrub Swamps	45	4·6	4·8
	46	6·1	5·0
	37	4·3	5·1

representing humus) and low pH. The plants of this community must tolerate a high water-table, with its resultant poor root aeration and high acidity. They are seldom subject to water shortage, although the surface soil to a depth of several inches occasionally becomes very dry in the higher parts of the community.

The floristics of this rather homogeneous community are set out below, the figures being those for eight quadrats each of one square metre. The numbers refer to each ascending shoot or cluster of vegetation; thus each ascending shoot of *Selaginella uliginosa* was taken as one unit, and each tussock of *Gymnoschoenus sphaerocephalus* is made up of from six to ten units, representing separate clusters of vegetation. Life forms are given for the vascular species, the seedlings of shrubs being classed as nanophanerophytes. Because of the density of the vegetation (Pl. ii, C), it was necessary to remove each shoot or plant with shears as it was counted.

Species.	Life-form.	Shoots per sq. metre for eight quadrats							
Fossombronia sp.	—	..	+	..	..	+	..	..	..
Sphagnum sp.	—	+	..	..	..	+	..	..	..
Dichaeta sp.	—	..	+	..	..	+	..	..	..
Lycopodium laterale	HH.	55	152	..	3	..	1	29	57
Selaginella uliginosa	H.	117	227	126	187	73	129	98	167
Schizaea bifida	HH.	..	1*	..	..	..	..	..	..
Entolasia marginata Hughes	H.	..	..	..	9	..	..	..	..
Chorizandra sphaerocephala	HH.	12	7	12	11	9	15	5	7
Gymnoschoenus sphaerocephalus	H.	18	12	12	46	46	21	17	31
Hypolaena lateriflora Benth.	H.	49	28	47	69	108	121	31	37
Lepidosperma Forsythii Hamilt.	HH.	54	94	36	67	11	5	51	47
Lepidosperma laterale	HH.	..	..	2	..	4	..	5	1
Leptocarpus tenax	HH.	..	5	17	15	11	29	3	15
Lepyrodia scariosa	HH.	7	5	30	..	1	27	5	13
Restio complanatus	HH.	10	4	2	19	..	21	5	11
Xyris gracilis	H.	..	5	7	35	5	21	..	6
Xanthorrhoea minor	H.	..	..	6	1	8	..	5	7
Banksia latifolia var. *minor*	N.	..	2†	..	..	..	..	1	..
Hakea pugioniformis	N.	1†	..	1†	1†	1†	..	1	..
Persoonia salicina	N.	..	..	1	..	..	..	..	..
Drosera pygmaea	Ch.	..	..	..	..	3	..	..	2
Viola hederacea	Ch.	..	..	..	3*	..	..	..	..
Baeckea linifolia	N.	..	1†	..	..	..	..	..	..
Epacris obtusifolia	N.	..	47†	..	..	2†	..	12†	..
Mitrasacme polymorpha	Ch.	..	..	19	10	20	11	..	15
Villarsia exaltata F.v.M.	Ch.	3†	2†	1†	..	..	4†	..	..
Utricularia lateriflora	Ch.	..	..	..	5	..	3	..	1
Goodenia bellidifolia	Ch.	..	..	30†	3†	24†	2†	15†	5†

* Weak plant. † Seedling. All apparently cryptophytic species are classed as helophytes.

From general inspection of other parts of this community, this table would appear to give a substantially correct picture of the floristics, except that *Banksia latifolia* (normal form) is as common as *B. latifolia* var. *minor*, and *Lepidosperma Forsythii* is generally less common than in the measured quadrats. In the lower parts of the swamp (Fig. 1), where the water-table is continuously at the surface, and where the water is usually moving in runnels or small creeks, *Leptospermum juniperinum* Sm. is developed in definite belts, sometimes with the addition of *Gahnia psittacorum*, rarely with a prominent belt of *Lepidosperma Forsythii*.

The community is exactly similar to the extensive 'Button-grass Plains' of Tasmania (especially important in western Tasmania and on the central plateau). The structure (tussocky vegetation 3–4 feet high, with smaller sedge-like vegetation and chamaephytic herbs at ground level, and occasional shrubs) is identical, and the most prominent species (*Gymnoschoenus sphaerocephalus*) is common to both. Many of the subsidiary species are common to both expressions of the community, though the Tasmanian development is, as would be expected, richer floristically, the present example being extra-limital.

Near the northern limit of the area studied, at Madden's Plains, equally extensive swamp-like tracts occur for two to three miles west of the scarp. The soil is here shallower than in the swamps immediately north of Sublime Point, rock level often being reached at 18 inches, and the conditions are throughout drier. The vegetation, which may be conveniently termed a 'moor', has more of the appearance of the 'shrub swamp' stage noted above (under wet lithosere). *Gymnoschoenus sphaerocephalus* is less, *Xanthorrhoea minor* more prominent, than in the swamps near Sublime Point. Shrubs are generally more abundant, those present in the Sublime Point swamps being increased in frequency, and others (e.g., *Melaleuca squarrosa*) added. In one sector, the Madden's Plains moor continues over a gentle rise to become continuous with the Sublime Point swamps immediately to the south.

The soils of the Madden's Plains moors are less subject to high water-table, and have a correspondingly lower organic content, although the pH is as low as in the Sublime Point swamps (Table 4).

These swamp and moor communities, both in the Bulli district and in Tasmania, are, surprisingly, very liable to fires. This is most likely in dry seasons, but even in rather damp weather a fire will 'run' through the *Gymnoschoenus sphaerocephalus* Community, each tussock of the dominant having always a basal residue of dead, combustible leaves. In the spring of 1935, almost the entire area of the swamps near Sublime Point, and parts of Madden's Plains, were swept by a fire which removed all the aerial parts of the vegetation. However, nearly all species of this community have hypogeal parts which, buried in wet soil, survived the fire. The sedge-like types possess submerged or half-submerged rhizomes, while some of the shrubs have subterranean root-stocks capable of regeneration. Within three weeks from the time of the fire, the rhizomes had begun to send up new shoots (Pl. ii, D); in one year the community had regained its normal appearance, both in height and structure, and floristically. The only noticeable change was the unexplained decrease in abundance of *Lepidosperma Forsythii* Hamilton.

The value of cryptophytic and hemicryptophytic life-forms in swamp communities subject to fire is obvious; fire here replaces the unfavourable season, resistance to which formed the original criterion on which Raunkiaer based his life-form classification.

In the Bulli district, the high rainfall and relatively low saturation-deficit of the eastern parts of the plateau, where these swamp communities occur, probably assist in the retention of swamp conditions; other parts of the coastal range (e.g., the mountains behind Bateman's Bay), where similar conditions of rain and mist prevail, possess similar extensive swamps. The regeneration of the swamp communities, after fire, to their former level, indicates that the reduction of saturation-deficit at the soil surface, due to the dense tangle of vegetation characteristic of these communities, is relatively unimportant in maintaining the communities in their present state. After fire, the vegetation being removed, there is no delay in evaporation due to vegetational cover; nevertheless, this temporary removal of the vegetation has no effect in raising the shrub element of the subsequent vegetation, or in altering the community in any way towards a drier state.

In Tasmania, the reasons for the high water-table conditioning this community are more dependent on climate (rainfall, saturation-deficit), and less on drainage-inhibiting topography, than in the present case. The *Gymnoschoenus sphaerocephalus* Community is so widespread in Tasmania as almost to justify its recognition as a climax formation (high moor), although the presence of neighbouring formations (sclerophyll forest, temperate rain-forest) where drainage is more efficient renders such a classification doubtful. The general preponderance of forest communities in the Bulli district, however, leaves no doubt that the *Gymnoschoenus sphaerocephalus* Community should there be regarded as a subclimax, widespread in extent, controlled topographically by poor drainage conditions. Causes of the high water-table, which in many cases is higher than the slope of the ground would otherwise allow, are the clay horizon at 4 feet depth (probably formed by the weathering of shale bands in the Hawkesbury Sandstone when these soils were originally formed, rather than by vertical

movement of the clay fraction), and the presence in many places of soil furrows at right angles to the slope (Pl. ii, B), impeding water flow. These furrows alternate with parallel ridges carrying tussocky vegetation, distant from one to two yards, the variation in height between peak and trough of the soil surface being 4–12 inches. The furrows were particularly apparent in a visual survey of the area from the air. The troughs of these furrows have a relatively low percentage cover by vegetation. Their origin may possibly be sought in the burrowing activities of swamp crayfish,* which are very common in this area; the troughs of the furrows are characterized by the presence of holes, the retreats of the crayfish. Once started, the maintenance of this system of furrows is not difficult to explain, the crayfish remaining in the moister and more congenial trough regions, the vegetation favouring the better-drained and less disturbed ridges. The initiation of the furrow system, with its surprising regularity, is more difficult to explain. It has not been observed in this community in Tasmania, where, however, crayfish of the same general habits are equally common.

In the swamps noted under 'wet lithoseres', the high water-table is usually due to the contour of the underlying rock; this does not apply in the Sublime Point swamps, where the soil is very deep (Fig. 1), and even at Madden's Plains, where the soil is shallower, the contour of the underlying rock is convex, and apparently would be ineffective in preventing lateral drainage.

Within the general area of the swamps, *Eucalyptus micrantha* Benth. develops wherever local conditions cause a lower water-table to occur (Pl. ii, E, F and G). These conditions are fulfilled in some cases by gentle hillocks or ridges, or above certain slight increases in the slope of the soil surface. Thus the *Eucalyptus micrantha* clump of Figure 1 (Pl. ii, F and G) is allowed by a relatively sudden, though still gentle, fall of the soil surface to the west of the clump (left in Figure 1) and to the north; the ground to the south of this clump carries the typical *Gymnoschoenus sphaerocephalus* Community, though it is on a slightly higher level than the clump. All such developments of *Eucalyptus micrantha* are bordered by a shrub zone (Pl. ii, F and G).

In the cases of two such clumps, younger trees of *E. micrantha* extend beyond the general outline. This would indicate a local forward succession, possibly caused by a fall in water-table following erosion of the soil below the clump, with a consequent increase in slope.

Throughout the swamp and moor communities, species of ants (*Myrmecia nigrocincta*, and others) form nests by raising dead leaves and sand grains onto the tussocky vegetation. Calcination of such nests leaves a residue of over 50% by weight. In the forest communities, especially at the ecotone of *E. micrantha* and swamp, these nests occur in considerable numbers, not raised, but on the surface of the drier soil. While this carriage of soil particles is discounted as a cause of local forward succession from swamp conditions, the effect of these ants in aerating the soil of swamp ecotone communities cannot be considered negligible.

On the rise between Madden's Plains and the Sublime Point swamps, in a typical moor community, young trees of *Eucalyptus gummifera* have developed during the last eight years (Pl. ii, H). The reason for this is unknown. It is very surprising to find this species apparently initiating a local succession to forest vegetation, instead of *E. Sieberiana* or *E. micrantha*, which are more tolerant of swamp conditions.

In conclusion, it may be stated that a general succession from these swamps and moors to forest can occur only when the drainage conditions are improved by a change in topography, by artificial drainage channels or by the gradual erosion of the plateau surface, e.g., further extension of the Loddon Falls gorge.

(*e*). *Vegetation of the Scarp.*

The vegetation of the scarp is efficiently sheltered from westerly winds, and from the sun after noon. Variations in the water-supply, from situations where the soil is continuously damp to those where it is usually very dry, account for the diversity of

* *Euastacus hirsutus* (McCulloch).

species encountered. As a whole, the vegetation may be regarded as a retrograde lithosere, growing in unstable circumstances. In general, dynamic equilibrium obtains between the normal processes of autogenic succession and the retrograde influences of soil denudation and falling rock.

Drier areas consist of bare rock, partly covered by mats of *Cyclophorus serpens*, *Polypodium Billardieri* and *Dendrobium linguiforme*, with the nanophanerophytes, *Xanthorrhoea arborea* R.Br. and *Actinotus Helianthi*, developing where sufficient soil is formed. Moister areas consist of a mosaic of bare rock, liverworts and mosses, and, where sufficient soil is formed, the following species:

N: (Shrubs, or trees less than six feet in height.) *Banksia ericifolia, Doryphora Sassafras, Callicoma serratifolia, Ceratopetalum apetalum, Pultenaea daphnoides, Cryptandra ericifolia, Pomaderris phillyroides, Backhousia myrtifolia, Leptospermum stellatum, Melaleuca hypericifolia, Tristania laurina, Dracophyllum secundum, Epacris coriacea, E. longiflora* and *Leucopogon lanceolatus*.

Ch: *Todea barbara, Billardiera scandens, Viola hederacea, Halorrhagis teucrioides, Xanthosia pilosa, X. tridentata*.

H: *Blechnum capense, B. Patersoni, Gleichenia dicarpa, Gahnia psittacorum, Hypolaena lateriflora* Benth. (N.B. Hemicryptophytic under these conditions; some of the species are cryptophytic in deeper soils.)

E: *Cassytha paniculata*.

The above species include some of the more mesophytic species of the *Eucalyptus Sieberiana* Association, some brush species, and a few swamp types restricted to seepage areas on the scarp.

(2). *Wianamatta Shale*.

Vegetation at Darkes' Forest may be classed as the *Angophora lanceolata* facies of the *Eucalyptus piperita* Association (Pl. i, F). Structurally, it represents high forest (80–100 ft.), canopy subdiscontinuous, with a prominent low-tree stratum, an almost continuous shrub stratum, and a ground stratum, continuous only where the shrubs are least dense. Floristically, its composition is as follows:

MM: A, *Angophora lanceolata, Eucalyptus piperita*; O, *Eucalyptus eugenioides, E. gummifera*; R, *Eucalyptus micrantha* Benth., *E. Sieberiana*.

M: C, *Acacia binervata, A. longifolia*; O, *Hakea saligna, Exocarpus cupressiformis, Rapanea variabilis* Mey.; R, *Acacia decurrens* var., *A. rubida, Leptospermum stellatum*.

N: A, *Banksia ericifolia, B. spinulosa, Persoonia salicina, Acacia myrtifolia*; C, *Hakea pugioniformis, Lambertia formosa, Acacia discolor, Pultenaea daphnoides, Dampiera Brownii*; O, *Hakea dactyloides, Lomatia silaifolia, Persoonia ferruginea, P. lanceolata, Leptomeria acida, Pimelea linifolia, Epacris pulchella, Olearia ramulosa* Benth.; R, *Banksia paludosa* R.Br., *Lomatia ilicifolia, Leucopogon esquamatus, L. lanceolatus, Cassinia aurea, Olearia viscidula* Benth.

N (climber): C, *Smilax glycyphylla, Kennedya rubicunda*.

Ch: C, *Doryanthes excelsa, Hibbertia Billardieri, Halorrhagis teucrioides*; O, *Schoenus imberbis, Glycine clandestina, Viola hederacea*; R, *Patersonia glauca*.

H: A, *Paspalum dilatatum* Poir. (introd.); C, *Culcita dubia, Blechnum cartilagineum, Lindsaya microphylla, Lomandra longifolia, Rubus fruticosus* (introd.).

G: C, *Pteridium aquilinum*; R, *Pterostylis nutans*.

Th: C, *Hypochaeris glabra* (introd.); O, *Poa annua* (introd.), *Gnaphalium purpureum*.

E: C, *Loranthus celastroides*.

Soil properties for this community are given in Table 5. They give no indication why the community should appear to be a sandstone one, enriched by a few more mesophytic species, rather than a true shale community. The absence of such trees as *Eucalyptus pilularis* and *Syncarpia laurifolia* Ten., characteristic of the Wianamatta Shale in other districts, is inexplicable. Trees of *Eucalyptus globulus*, introduced in this area, flourish at Darkes' Forest.

(3). *Narrabeen Series*.

In some areas between Bulli Lookout and Broker's Nose, the Hawkesbury Sandstone beds have been removed by erosion to expose the Narrabeen beds (Part i, Pl. xv). These latter consist of an upper layer of Chocolate Shale some 50 feet in depth, below which is a considerable thickness of rather fine-grained Narrabeen Sandstone. Erosion

TABLE 5.

Properties of Soils of Wianamatta and Narrabeen Series.

——	W.R.C. (%).	Loss on Ignition (%).*	pH.
Wianamatta Shale.			
Eucalyptus piperita Association (*Angophora lanceolata* facies)	91	28	5·0
	91	25	5·1
	97	24	5·5
Narrabeen Sandstone.			
Eucalyptus piperita Association, no physiographic shelter	50	18	5·6
Eucalyptus saligna Association, partial physiographic shelter	58	31	5·6
Chocolate Shale.			
Eucalyptus saligna Association, no physiographic shelter	53	16	5·6
	60	14	6·3
	62	16	5·2
	71	16	5·2
	76	23	5·9
Brush, partial physiographic shelter ..	100	39	5·5
	130	36	5·3

* Only a small fraction of this figure represents humus.

A_2 Horizon.

Derivation of Soil.	Water Held at Sticky-Point (%).	Sand Fraction (%).	Index of Texture.
Wianamatta Shale	49·0	82	33
	50·1	83	33
	53·0	72	39
	55·0	70	41
Chocolate Shale	46·4	94	28
	49·0	92	31
	50·7	89	33
Narrabeen Sandstone, relatively pure.. ..	30·0	93	11
Narrabeen Sandstone, contaminated with Chocolate Shale	45·0	95	26
	46·7	95	28

of these beds is only incipient, and the Chocolate Shale weathers more rapidly than the underlying sandstone; under these circumstances, it is impossible to find a Narrabeen Sandstone soil uncontaminated with at least a small fraction of the shale soil. This, and the variation in slope and shelter, lead to some confusion in the arrangement of communities. It appears that on the least contaminated of the Narrabeen Sandstone soils, *Eucalyptus piperita* is dominant in unsheltered situations, with *E. eugenioides*, *E. gummifera*, *E. pilularis* and *E. saligna* of occasional occurrence, *E. paniculata* and *E. Sieberiana* rare. On the soils of the Chocolate Shale (except where physiographic shelter leads to the development of brush), and in moderately sheltered positions on the Narrabeen Sandstone, *Eucalyptus saligna* is dominant, with *E. pilularis* and *Syncarpia laurifolia* Ten. common, and *E. eugenioides*, *E. paniculata* and *E. piperita* rare. Introduced pine-trees (*Pinus radiata*) also occur in these communities.

The structure of these communities, which may be termed the *Eucalyptus piperita* and *E. saligna* associations respectively, is similar to the Darkes' Forest (Wianamatta Shale) community. Soil properties are shown in Table 5. The following represents a reasonably complete estimate of the floristics, most species being common to both associations:

MM: See above.

M: C, *Exocarpus cupressiformis*, *Acacia longifolia*, *A. mollissima*: R, *Hakea saligna*.

N: A, *Persoonia salicina*, *Idigofera australis*, *Pomaderris elliptica*, *Pimelea ligustrina*, *Prostanthera Sieberi* Benth.; C, *Banksia spinulosa*, *Persoonia ferruginea*, *P. lanceolata*, *Acacia discolor*, *A. suaveolens*; O, *Persoonia revoluta*, *Acacia myrtifolia*, *Zieria Smithii*, *Astrotricha floccosa*, *Cassinia longifolia*; R, *Persoonia linearis*, *Pultenaea daphnoides*, *Dodonaea triquetra*, *Lasiopetalum ferrugineum*, *Helichrysum diosmifolium*, *H. elatum*; VR, *Xylomelum pyriforme*, *Citriobatus multiflorus*, *Pultenaea flexilis*.

Ch: C, *Hibbertia Billardieri*, *Halorrhagis teucrioides*; O, *Kennedya rubicunda*, *Viola hederacea*; R, *Billardiera scandens*, *Geranium pilosum*.

H: LC, *Blechnum cartilagineum*, *Imperata cylindrica* var. *Koenigii*, *Paspalum dilatatum* Poir. (introd.), *Rubus fruticosus* (introd.); O, *Cynodon dactylon*; R, *Culcita dubia*, *Eragrostis Brownii*, *Stipa pubescens*.

G: A, *Pteridium aquilinum*.

Th: O, *Poa annua* (introd.), *Hypochoeris glabra* (introd.); R, *Gnaphalium luteo-album*, *G. purpureum*.

E: O, *Loranthus celastroides*, *Cassytha paniculata*; VR, *Cymbidium suave*.

In conditions of partial shelter from the west, brush develops on the Chocolate Shale; this formation occurs in efficient shelter on the Narrabeen Sandstone. It is structurally similar to the coastal brush to be described in the next part of this series. The only species present in the brush of the Narrabeen beds on the plateau area yet absent from the brush of the coastal slopes is the tree-fern, *Dicksonia antarctica*.

In parts of the *Eucalyptus saligna* Association (supra), where shelter is slightly too inefficient for true brush to develop, some species (e.g., *Livistona australis*, *Alsophila australis*) are added, giving the vegetation the nature of an ecotone community.

Around the borders of Cataract Reservoir (Pl. i, I), the vegetation shows a regular zonation conditioned by artificial raising of the water-table. *Myriophyllum propinquum* A. Cunn. is the chief representative of the floating stage; occasionally, fall in water level in the reservoir leaves this species on the drying mud surface, where it persists for a time as a land plant, usually forming red pigment. Near the upper limit of the water a hemicryptophytic zone occurs, with *Juncus pallidus*, *J. bufonius*, *Poa annua* (introd.), *Gratiola Peruviana* and, further back, *Imperata cylindrica* var. *Koenigii*. When expanses of mud are exposed below this zone by a fall in water level of long duration, therophytes temporarily colonize it (e.g., *Centipeda minima* A.Br. et Aschers, *Erigeron crispus* Pourret (introd.)). Behind the hemicryptophytic zone, the *Eucalyptus saligna* Association is present, shrubs of *Melaleuca squamea* and *Leptospermum flavescens* occupying an intermediate position where the high water-table inhibits tree development.

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EXPLANATION OF PLATES I-II.

Plate i.

A.—*Eucalyptus Sieberiana* Association on Hawkesbury Sandstone, south of Cataract Reservoir.

B.—*Eucalyptus Sieberiana* Association on Hawkesbury Sandstone, south of Sublime Point. The soil is rather shallow, and rock outcrops occur.

C.—*Eucalyptus piperita* Association on Hawkesbury Sandstone, upper slopes of gully south of Cataract Reservoir.

D.—*Eucalyptus pilularis* Association on Hawkesbury Sandstone, lower slopes of gully south of Cataract Reservoir.

E.—Depauperate brush (subtropical rain-forest formation) on Hawkesbury Sandstone, bottom of Loddon Falls Gorge.

F.—*Eucalyptus piperita* Association (*Angophora lanceolata* facies) on Wianamatta Shale soil, Darkes' Forest.

G.—First stages of zonation from exposed Hawkesbury Sandstone rock under moist soil conditions (moist lithosere); mosses, and *Lepyrodia scariosa*. Near Loddon Falls.

H.—Moist lithosere near Loddon Falls. Hawkesbury Sandstone outcrop in foreground, leading by moss and 'hemicryptophyte' stages to swamp and forest. Trees with pale trunks in middle distance are *Eucalyptus micrantha* Benth., passing to *Eucalyptus Sieberiana* Association in background.

I.—Zonation beside Cataract Reservoir, Narrabeen Series.

Plate ii.

A.—*Gymnoschoenus sphaerocephalus* Community north of Sublime Point.

B.—Natural contour furrows in *Gymnoschoenus sphaerocephalus* Community north of Sublime Point. The position of the furrows is indicated by oblique lines of darker vegetation, corresponding to the wetter nature of the soil.

C.—Metre quadrat in *Gymnoschoenus sphaerocephalus* Community, north of Sublime Point.

D.—*Gymnoschoenus sphaerocephalus* Community north of Sublime Point, regenerating after a fire which had removed all aerial parts one month previously. *Gymnoschoenus sphaerocephalus* and *Xanthorrhoea minor* shooting from hypogeal remains.

E.—Clump of trees of *Eucalyptus micrantha* Benth. surrounded by *Gymnoschoenus sphaerocephalus* Community, south of Cataract Reservoir. Note young tree on left of clump.

F, G.—Clump of young trees of *Eucalyptus micrantha* Benth. in *Gymnoschoenus sphaerocephalus* Community north of Sublime Point. The zone of shrubs outlying the trees corresponds to intermediate conditions of water-table (cf. Fig. 1).

H.—*Gymnoschoenus sphaerocephalus* Community at Madden's Plains, with bushes and young trees of *Eucalyptus gummifera* developing.

Appendix.

Life-Form Spectra for Communities of Plateau.

	MM.	M.	N.	Ch.	H.	G.	HH.	Th.	S.	E.	No. of Species.
Eucalyptus Sieberiana Association ..	4	5	54	19	11	5	..	..	..	2	130
Swamp and Shrub Swamp (moist lithosere)	..	..	43	22	18	..	13	3	..	1	74
Gymnoschoenus sphaerocephalus Community	..	..	20	24	24	..	32	..	..	..	25
Eucalyptus piperita Association (*Angophora lanceolata* facies) ..	12	14	42	12	10	3	..	5	..	2	59
Eucalyptus saligna and *E. piperita* Associations (Narrabeen Series)	15	7	41	10	13	2	..	7	..	5	59

PLANT ECOLOGY OF THE BULLI DISTRICT.

PART III: PLANT COMMUNITIES OF THE COASTAL SLOPES AND PLAIN.

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(Plates iii–iv.)

[MS. received 9th February, 1940. Read 26th March, 1941.]

(1). Eucalyptus pilularis *Association.*

This community occupies soils of the Narrabeen Sandstone and Upper Coal Measures on the coastal slopes and plain where conditions are not favourable for the development of brush (subtropical rain-forest) or brush ecotone communities. One exception is the community occurring on soils derived from tuffaceous mudstone (Upper Coal Measures) at Towrodgie (infra). Settlement has caused destruction or alteration of large areas of the *Eucalyptus pilularis* Association, much of the community as it exists at present representing second-growth timber of the dominant. Even where the high trees are untouched, the lower strata are often much altered by clearing and grazing, fire, and introduced plants. Areas from which the dominant has been entirely cleared have been omitted from the present study.

Structurally, the community (Pl. iv, A) comprises a high tree stratum of the dominant, together with *Eucalyptus paniculata* and *Syncarpia laurifolia* Ten., reaching over 150 feet in height in some cases; the canopy is never continuous. Mesophanerophytes (*Casuarina torulosa, Acacia binervata*) are moderately frequent on the slopes; microphanerophytes are seldom prominent. The shrub layer is rather sparse; the ground layer, chiefly hemicryptophytic, is almost continuous except on the driest ridges.

Soil properties (Table 1; for methods, see Part ii of this series) exhibit a wide range. The lowest figures for water-retaining capacity (30–36%) show no improvement over the Hawkesbury Sandstone soils of the plateau (cf. *Eucalyptus Sieberiana* Association, Part ii of this series), but the lower (e.g., B) horizons of the Upper Coal Measures soils show a marked increase in water-retaining capacity over the surface soils to which Table 1 applies.

TABLE 1.
Soil Properties for Eucalyptus *Associations of Coastal Slopes and Plain.*

——	W.R.C. (%).	Loss on Ignition (%).	pH.
Eucalyptus pilularis on soils of Upper Coal Measures (Shales and Sandstones) ..	30	2·8	6·2
	34	7·2	5·8
	36	10·0	5·5
	49	5·3	5·7
	49	9·2	5·5
	69	4·8	6·2
	69	11·0	5·8
Mixed *Eucalyptus* Forest on tuffaceous mudstone soil, Upper Coal Measures	53	14·0	5·5
	88	18·0	5·2
	97	19·0	5·2
Mixed *Eucalyptus* Forest on recent alluvial soil (climax to subsaline lagoon succession) ..	63	13·0	6·3
	71	14·0	6·3
	83	18·0	6·1
	91	20·0	6·0

The following is a floristic estimate of the less disturbed parts of this association:

MM: A* (dominant), *Eucalyptus pilularis*; C, *Casuarina torulosa* (slopes only), *Eucalyptus paniculata, Syncarpia laurifolia* Ten.; O (LC), *Acacia binervata*,

* Abbreviations for life-form, frequency, and localization, as in Part ii of this series.

Eucalyptus eugenioides (plain only), *E. saligna* (brush ecotone dominant); VR, *Eucalyptus botryoides*.

M: O, *Persoonia linearis, Leucopogon lanceolatus, Rapanea variabilis* Mey., *Notelaea longifolia*; R, *Elaeocarpus reticulatus*; VR, *Acacia mollissima*.

N: A, *Acacia myrtifolia, A. suaveolens*; C, *Persoonia salicina, Indigofera australis, Oxylobium trilobatum, Pimelea ligustrina, Goodenia ovata, Helichrysum diosmifolium, Senecio dryadeus* Sieb.; O, *Zieria Smithii, Sida rhombifolia, Prostanthera Sieberi* Benth., *Helichrysum bracteatum* Willd., *H. elatum, Olearia ramulosa* Benth.; O (L), *Hakea pugioniformis, Citriobatus multiflorus, Leptospermum flavescens, Lantana camara* (introd); R, *Pimelea linifolia, Cassinia denticulata, Olearia argophylla* F.v.M.; VR, *Phyllota phylicoides, Pultenaea flexilis*.

N (climbers): C, *Smilax glycyphylla, Clematis aristata, Billardiera scandens*; O, *Geitonoplesium cymosum*.

Ch: A, *Hardenbergia monophylla, Hibbertia dentata*; C, *Viola hederacea, Plantago lanceolata* (introd.); O, *Dianella longifolia, D. revoluta, Glycine clandestina, Geranium pilosum, Hibbertia Billardieri, Halorrhagis teucrioides, Astroloma humifusum*; R, *Dianella coerulea, Hypoxis hygrometrica, Tillaea Sieberiana* Schultes, *Bossiaea prostrata*; VR, *Desmodium varians, Plantago varia*.

H: A, *Paspalum dilatatum* Poir. (introd.), *Rubus fruticosus* (introd.); C, *Doodia aspera, Cynodon dactylon, Eragrostis Brownii* (including var. *patens*), *Imperata cylindrica* var. *Koenigii, Carex paniculata, Lomandra longifolia* Labill.; LC, *Selaginella uliginosa*; O, *Themeda australis* Stapf., *Lomandra multiflora* Britt., *Oxalis corniculata*; O (L), *Adiantum aethiopicum, Asplenium flabellifolium*; R, *Blechnum cartilagineum, Calamagrostis quadriseta* Spreng., *Oplismenus compositus, Poa caespitosa*; VR, *Stipa pubescens, Luzula campestris, Lomandra filiformis* J. Britten.

G: A, *Pteridium aquilinum*; O, *Schelhammera undulata, Caladenia carnea, Dipodium punctatum, Pterostylis nutans*; O (L), *Burchardia umbellata, Microtis porrifolia*; R, *Tricoryne simplex, Caladenia alba*; VR, *Schizaea dichotoma, Calochilus campestris, Pterostylis ophioglossa*.

E: C, *Loranthus celastroides*; O, *Cassytha paniculata*; VR, *Cassytha glabella*.

Th: A, *Hypochoeris glabra* (introd.); C, *Wahlenbergia gracilis, Gnaphalium japonicum, Sonchus oleraceus* (introd.); O, *Poa annua* (introd.), *Phytolacca octandra* (introd.), *Anagallis arvensis* (introd.), *Erythraea australis, Solanum nigrum, Gnaphalium luteo-album, G. purpureum, Taraxacum officinale* Weber (introd.); R, *Stellaria flaccida, Erechthites arguta* DC.

On the wider parts of the coastal plain (e.g., near Corrimal) both *Syncarpia laurifolia* Ten. and *Eucalyptus eugenioides* assume a position of local dominance in a few cases. *Casuarina torulosa* is absent from these areas, being characteristic of the slopes. *Eucalyptus saligna* is not a typical member of this association, being rather the dominant of the brush ecotone community, which might almost be considered as part of the *Eucalyptus saligna* Association noted in Part ii of this series.

The absence of such trees as *Eucalyptus gummifera* and *E. Sieberiana* from the sclerophyll forests of the slopes and plain is somewhat surprising; it may be due to the higher pH of these areas (5·5–6·2, as opposed to 4·9–5·4 for soils carrying these species on the plateau), or to competition.

Mixed Eucalyptus Forest.

On the north side of Towrodgie Creek a Mixed *Eucalyptus* Forest occurs on soils derived from a tuffaceous mudstone, a local representative of the Upper Coal Measures. Soils from this situation are finer in texture* than is normal for the Upper Coal

* Samples from the A_2 horizon of the mudstone soil and of other Upper Coal Measures soils have the following properties:

——	Water Held at Sticky-Point (%).	Sand Fraction (%).	Index of Texture.
Mudstone	37·5	85	20
	38·0	84	21
Other Upper Coal Measures soils	19·0	88	2
	19·5	87	3
	25·9	95	7
	44·6	71	31
	45·0	70	31

Measures, but this does not adequately explain the difference between the vegetation and the normal *Eucalyptus pilularis* Association. The area is close to the sea, and only a slight distance above the level of a subsaline lagoon; however, on the south side of Towrodgie Creek a pure stand of *Eucalyptus pilularis* is developed on soil derived from Upper Coal Measures shale, in an otherwise exactly comparable situation.

The trees of this mixed forest are lower than those of the *Eucalyptus pilularis* Association, and somewhat gnarled (Pl. iv, B), possibly as a result of sea-winds. Co-dominants are *Eucalyptus eugenioides*, *E. longifolia*, *E. paniculata* and *E. punctata*, with *E. botryoides* occurring occasionally. The lower strata, when undisturbed, resemble those of the *Eucalyptus pilularis* Association, including low trees of *Notelaea longifolia*, shrubs of *Acacia myrtifolia*, *Oxylobium trilobatum* and *Pimelea linifolia*, and a ground layer of *Pteridium aquilinum*, *Cynodon dactylon*, *Burchardia umbellata* and annuals such as *Hypochoeris glabra*, as its most important members. To these are added elements of the seres discussed below (e.g., *Leucopogon Richei* and *Hibbertia volubilis* from the psammosere, and *Gahnia psittacorum* from the subsaline hydrosere), and a few brush species (e.g., *Clerodendron tomentosum*).

The whole community agrees closely with the neighbouring Mixed *Eucalyptus* Forest occurring on recent alluvial soils, and interpreted as climax of the lagoon sere. This resemblance may possibly be explained by the assumption that the soil in the present case, though derived from the underlying rock, has in the recent past been partly flooded by lagoon waters, which have since been lowered by allogenic causes.

(2). *Brush* (*Subtropical Rain Forest*).

Brush is developed on soils derived from the Narrabeen Sandstone and Upper Coal Measures wherever sufficient shelter occurs, usually in situations with a copious supply of soil water. The formation occurs on the Chocolate Shale on the dissected parts of the plateau, tolerating on soils of this rock type either situations of efficient shelter, but low average soil moisture (e.g., immediately below the top of Bulli Pass), or situations with slight shelter from the west, but with a better supply of soil moisture (e.g., immediately west of the top of Bulli Pass; Davis, 1936, Pl. xv, J). Development of brush on Hawkesbury Sandstone soils is limited to areas of extreme shelter (cf. Part ii of this series).

Three main factors, then, enter into the conditioning of brush development. (1) Physiographic shelter from dry (westerly) winds and, to a less extent, from insolation; (2) supply of soil moisture, dependent on drainage and evaporation; and (3) soil type as conditioned by parent rock. Factors (2) and (3) react together to some extent to govern the ultimate soil type, moisture supply governing humus formation, which, with the texture of the soil as formed from rock decomposition, determines the water-retaining capacity.

Considering these three variables, two facts seem clear: (i) Brush is able to develop in situations of decreasing shelter on soils of increasing fineness of texture; the series Hawkesbury Sandstone-Narrabeen Sandstone-Upper Coal Measures-Chocolate Shale seems to apply. The last-named soils have, it is true, a coarser texture than some of those of the Upper Coal Measures, yet there seems no doubt that they are the best soils of this district. Chemical as well as physical properties of the soils may explain this fact. (ii) Shelter from wind and sun seems more important than soil conditions in brush development. Thus, for the soils listed in Table 2, only low-grade brush (practically equivalent to the *Eucalyptus saligna* ecotone Community) develops on the last soil listed, which, with partial physiographic shelter, has better properties than the seventh soil listed, a dry, well-drained soil carrying highly-integrated brush in a position of extreme shelter. However, the fifth and sixth soil-samples listed, with excellent properties, carry highly-integrated brush with very slight shelter from the west.

Brush develops on the upper coastal slopes, immediately below the scarp, except on several prominent ridges, where the *Eucalyptus pilularis* Association or *E. saligna* ecotone Community reaches the scarp. These upper slopes correspond to Narrabeen

Sandstone; Chocolate Shale exposures are very limited in extent on the slopes, except where the protecting Hawkesbury Sandstone cover has been entirely removed, as at the top of Bulli Pass. Soils of the upper slopes, at the level of the Narrabeen Sandstone, are contaminated with soil derived from overlying series, most markedly where erosion of the soft Chocolate Shale has been permitted by removal of the Hawkesbury Sandstone.

TABLE 2.

Properties of Soils carrying Brush (or Subtropical Rain Forest).

—	W.R.C. (%).	Loss on Ignition (%).*	pH.
Hawkesbury Sandstone, extreme shelter ..	90	30·0	5·2
	120	35·0	5·2
	120	49·0	5·3
	130	48·0	5·0
Chocolate Shale, partial shelter on plateau ..	100	39·0	5·5
	130	36·0	5·3
Easterly Slopes: soil derived chiefly from Chocolate Shale, very efficiently drained; extreme shelter.	60	21·0	5·8
	66	13·0	5·8
Easterly Slopes: soil derived from Narrabeen Sandstone mixed with talus from formations above; soil moisture high; shelter extreme to moderate.	200	38·0	6·9
Partial shelter; soil as above: Low-grade Brush.	61	9·4	5·9

* From 20% to 60% of this figure represents humus.

On the lower slopes, brush is restricted to gullies and to the inner (western) side of the larger terraces. Depauperate brush occurs beyond these limits, and probably many parts of the coastal plain once carried a brush element, prior to disturbance following settlement. The alternation of brush, sclerophyll and ecotone communities has been studied in a belt-transect between the 200-ft. contour and the scarp at Coledale; true brush extended down to the inner side of a terrace a little above the 400-ft. contour; below this, ecotone communities were present on terraces, but sclerophyll forest characterized other parts of the ridge followed. In a transect at right angles to the above, between two ridges running down from the upper slopes to the sea, brush was developed only at the lowest point, ecotone vegetation on the ridge facing south (except at its summit), sclerophyll forest on the summits of both ridges and on all except the lowest part of the north-facing ridge.

The brush studied has the characteristic facies of this formation as found in other parts of the State, namely a variety of trees of medium height, mostly laurel-leaved, with continuous canopy; paucity of small trees in most cases, except the tree-fern *Alsophila australis*; almost complete absence of shrubs, and presence of a discontinuous ground layer composed chiefly of ferns. In addition, epiphytes and climbers are common.

Omitting high sclerophyllous trees which occasionally grow in the brush, penetrating the canopy (*Eucalyptus pilularis*, *E. saligna*, and more rarely *Syncarpia laurifolia* Ten., *Eucalyptus paniculata* and *E. quadrangulata* Deane and Maiden), and the elements characteristic of the brush-sclerophyll forest ecotone, but absent from the true brush, the floristics may be set out as follows:

MM: A, *Livistona australis*, *Ficus stephanocarpa* Warb., *Doryphora Sassafras*; C, *Ficus rubiginosa*, *Laportea gigas*, *Pennantia Cunninghamii*, *Cryptocarya glaucescens*, *Endiandra Sieberi*, *Callicoma serratifolia*, *Pittosporum undulatum*, *Ceratopetalum apetalum*, *Omalanthus populifolius*, *Sloanea australis*, *Eugenia Smithii*, *Trochocarpa laurina*, *Sideroxylon australe*, *Cargillia australis* R.Br.; O, *Archontophoenix Cunninghamiana* Wendl. et Drude, *Polyosma Cunninghamii*, *Schizomeria ovata*,

Pittosporum revolutum, Claoxylon australe, Diploglottis Cunninghamii, Brachychiton acerifolius F.v.M., *Eugenia myrtifolia, Panax Murrayi, Clerodendron tomentosum*; R, *Mollinedia macrophylla, Cryptocarya microneura, Tristania laurina*; VR, *Podocarpus elata, Pisonia Brunoniana, Quintinia Sieberi, Melia Azedarach.*

MM (climbers): C, *Smilax australis, Clematis glycinoides, Sarcopetalum Harveyanum, Stephania hernandifolia, Palmeria scandens, Lyonsia straminea, Tecoma pandorana* Skeels, *Senecio mikanioides* Otto (introd.); O, *Piper hederaceum, Vitis hypoglauca, Lyonsia reticulata*; R, *Tylophora barbata.*

M: A, *Alsophila australis*; C, *Panax sambucifolius, Psychotria loniceriodes*; O, *Drimys insipida* Druce, *Sambucus xanthocarpa*; R, *Croton Verreauxii, Phyllanthus Gastroemii, Backhousia myrtifolia.*

M (climbers): C, *Eustrephus latifolius* R.Br., *Rubus parvifolius*; O, *Rubus Moluccanus, R. Moorei*; R, *Rubus rosifolius, Passiflora Herbertiana, Panax cephalobotrys.*

N: A, *Lantana camara* (introd.) (chiefly in disturbed areas); O, *Citriobatus multiflorus*; R, *Abrophyllum ornans.*

H: A, *Adiantum aethiopicum, A. formosum, Asplenium flabellifolium, Polystichum aculeatum*; C, *Blechnum capense, B. Patersoni, Pellaea falcata*; O, *Adiantum diaphanum, Dryopteris decomposita, Hypolepis tenuifolium, Sisyrinchium paniculatum*; R, *Adiantum hispidulum.*

G: A, *Gymnostachys anceps*; C, *Histiopteris incisa, Pteris umbrosa.*

E: A, *Cyclophorus serpens, Pleopeltis diversifolia, Peperomia reflexa, Arthropteris tenella, Hymenophyllum tunbridgense*; C, *Polypodium Billardieri*; O, *Davallia pyxidata, Cymbidium suave, Sarcochilus falcatus*; R, *Asplenium nidus, Platycerium bifurcatum*; VR, *Tmesipteris tannensis.*

The ecotone between the brush and the *Eucalyptus pilularis* Association is dominated by *Eucalyptus saligna*, and contains the more tolerant of the species of the true brush (e.g., *Livistona australis, Omalanthus populifolius, Alsophila australis, Lantana camara, Rubus parvifolius*), together with certain species confined to the ecotone, and not extending into the true brush except in cleared spaces. The low trees, *Breynia oblongifolia, Eupomatia laurina, Synoum glandulosum* and *Rhodamnia trinervia*, fall in this category, and the higher *Acacia binervata*, which can stand drier conditions, is frequently prominent. The climbers, *Smilax glycyphylla* and *Eustrephus latifolius* R.Br., occur in this ecotone community, together with a ground layer including *Adiantum aethiopicum, Oplismenus compositus, Pollia cyanococca, Urtica incisa, Rubus fruticosus* (introd.), *Stellaria flaccida, Plectranthus parviflorus* and *Brunella vulgaris* L.

The present record of a sample of the Illawarra brush indicates that it is poorer floristically than the brush forests of northern New South Wales (cf. Fraser and Vickery, 1938). The list given is probably not complete, even for the area studied, but there can be no doubt that a number of species of this northern formation fail to reach as far south as the Bulli district. Some species (e.g., *Cedrela australis*) known to have occurred in the district in the past have not been met with; *Cedrela* may be extinct in the district (by reason of the demand for its timber), though specimens occur in the Gerringong area, a little to the south. Other brush species (e.g., *Pseudomorus Brunoniana*) have been found further to the south (Cambewarra Range), but have not yet been recorded near Bulli.

(3). *Sand-Dune Succession.*

Consideration of sand-dune succession (psammosere), and the succession from subsaline lagoons (infra) must involve an account of recent movements of the strand-line. On a stable coast, both successions must ultimately reach a state of dynamic equilibrium between the upgrade tendencies of autogenic succession and the retrograde influences of wind action, marine erosion, and scouring by creeks. The district studied has no rivers discharging into the sea, so that the additional factor of the continual addition to the coast, of alluvium, may be neglected almost entirely.

It seems reasonably certain from other sources of information that the portion of coastline under consideration has been subjected, during the last 3,000 years, to a fall in sea-level of some 15 feet (see, e.g., Cotton, 1926). This has probably been gradual, extending over the whole period, and possibly continuing at the same rate, though evidence of this is lacking. In any event, this fall has converted shallow estuaries and bays into land-locked lagoons some feet above sea-level; on the outer side of these

lagoons are belts of dunes, possibly sand-bars of the former bays and estuaries. The lagoons reach the sea through breaks in these dunes, although difficulty of access to the sea usually maintains them at a level some feet above the sea; they are consequently not tidal or as saline as sea-water.

This slow allogenic action has given rise to new areas for plant colonization, and the vegetation of the dunes now appears to be reasonably stable, evidences of forward succession possibly referring to progress allowed by the more recent stages in the fall in sea-level. There is a certain amount of local retrogression, probably compensated by local succession in other sectors.

The zonation of the dune communities may thus be considered as a forward succession, probably brought to a standstill by the absence or extreme slowness of further change in the strand-line, and the inability of the pioneer stages of the vegetation to advance any further seaward (Pl. iii, C).

The sand-dune communities may be listed as follow:

(1). Festuca litoralis-Spinifex hirsutus-Carex pumila *Associes.*

This is the first community to develop, or, in terms of space, the most seaward. The first two species are of regular occurrence, *Carex pumila* being less common; it is questionable whether it deserves to rank in the naming of the associes, although, in certain dunes studied by the author in southern Tasmania, it and *Festuca* were equally important in this stage, while *Spinifex* was absent. The therophyte, *Cakile maritima,* occurs in and just below this community.

Festuca is a tussock-plant, and is most important in holding the sand against wind erosion on colonized areas, often remaining on sand hummocks when the surrounding sand at that level has been removed. *Spinifex,* with creeping stolons, is more important as a colonist of new areas, or areas which have been eroded. The rôles of these two species may therefore be regarded as passive and active respectively, in regard to soil stabilization (Pl. iii, A and C). On account of its greater mobility, *Spinifex* usually extends some distance beyond the seaward limit of *Festuca.*

(2). *Shrub-Dune.*

This community is dominated by shrubs of *Leptospermum laevigatum, Leucopogon Richei,* and *Acacia Sophorae* (Labill.) R.Br., with *Banksia integrifolia* in the shrub stage. The chamaephyte element (especially *Mesembryanthemum aequilaterale* and *Hibbertia volubilis*) occasionally forms a 'mat' stage extending seaward beyond the shrub line.

The shrub-dune represents the highest level of the dune area (Pl. iii, B), the ground behind it falling in level to the next stage (dune forest). The following is a floristic list for the shrub-dune:

N: A, *Leptospermum laevigatum, Leucopogon Richei*; C, *Banksia integrifolia* (bush), *Acacia Sophorae* R.Br.; LC, *Lantana camara* (introd.); O, *Atriplex cinereum, Monotoca scoparia, Senecio lautus*; R, *Correa alba.*

Ch: C, *Mesembryanthemum aequilaterale, Hibbertia volubilis*; O, *Commelina cyanea, Rhagodia hastata, Tetragonia expansa, Pelargonium australe, Calystegia Soldanella* R.Br.; R, *Rhagodia baccata* Moq.

H: C, *Cynodon dactylon*; O, *Sporobolus virginicus, Scirpus nodosus, Dichondra repens*; R, *Imperata cylindrica* var. *Koenigii, Lomandra longifolia* Labill., *Oxalis corniculata.*

G: O, *Pteridium aquilinum.*

Th: O, *Sonchus oleraceus* (introd.), *Onopordon Acanthium* (introd.).

(3). Eucalyptus botryoides-Banksia integrifolia *Associes.*

On the inner slope leading down from the shrub-dune, and in sandy hollows still further from the sea, a forest dominated by *Banksia integrifolia* and *Eucalyptus botryoides,* usually some 40 feet in height, occurs. All elements of the shrub-dune stage occur in this forest, in approximately the same proportions. *Eucalyptus longifolia* and *Banksia serrata* occur rarely as low trees. Additional species include:

M: *Pittosporum undulatum, Acacia linearis, Synoum glandulosum, Breynia oblongifolia, Cupaniopsis anacardioides* Radlk., *Clerodendron tomentosum.*

M (climbers): *Lyonsia straminea, Tylophora barbata.*

N: *Sida rhombifolia* (occasionally chamaephytic), *Pimelea linifolia*, *Brachyloma daphnoides*.
N (climbers): *Geitonoplesium cymosum*, *Stephania hernandifolia*.
Ch: *Viola hederacea*, *Halorrhagis teucrioides*.
H: *Themeda australis* Stapf., *Rubus fruticosus* (introd.).
E: *Cassytha paniculata*.

No climax Mixed *Eucalyptus* Forest occurs on dune soils in this area.

Retrograde factors adversely influencing the succession are marine erosion (action of waves during storms on the outer parts of the *Festuca-Spinifex-Carex* stage); wind erosion or blow-outs affecting chiefly the pioneer stage, where the soil is least efficiently stabilized, but sometimes affecting the higher stages, e.g., dune forest, after the intermediate stages have been removed (cf. Pl. iii, D); swamping of vegetation by drifting sand loosened by the preceding factor (affecting the dune forest community on the inner slope of the dunes, and noted to occur in many parts of the area); and erosion by the waters of lagoons, when they effect outflow to the sea (cf. Pl. iii, E). Opposed to these factors are the normal upgrade tendencies typical of any psammosere, namely, soil stabilization by vegetational cover, and improvement of the soil (especially with regard to water-retaining capacity) by the addition of organic remains. Proof of retrogression in some sectors is a matter of direct observation; proof of forward succession in other areas is deduced from examination of soil profiles with an auger, the soil of all stages passing, with increase in depth, to dune sand, by decrease of the percentage of organic matter.

Properties of surface soils in this psammosere are listed in Tables 3 and 3A. They indicate the increasing water-retaining capacity of the sere, due to accumulation of organic remains. Hydrogen peroxide tests indicate that the ratio of humus content to loss on ignition is 5–8% for the *Spinifex-Festuca-Carex* stage, 40% for the shrub-dune, 50% or a little over for the dune forest. Variations in chloride content, and in water-content (Table 3A) seem to be due to differences in drainage and leaching, the *Festuca* hummocks and the shrub-dune, on the dune crest, being efficiently drained and leached, part of the chloride leached from the latter passing to the dune forest soil on the inner slope. The soil of the dune forest, with its higher water-retaining capacity, would be less affected by percolation and leaching. Spray incidence is probably not greatly different in the various stages, but the lowest parts of the *Spinifex* zone occasionally come under the effect of waves. There is scarcely any significant change in pH throughout the sere, probably because of the buffering action of salts.

TABLE 3.
Soil Properties for Sand-Dune Succession.

——	W.R.C. (%).	Loss on Ignition (%).	pH.	Cl. (%).
Beach Sand	22	3·2*	6·6	0·05
Spinifex-Festuca Associes	24	0·6*	6·5	0·01
Spinifex	24	0·5*	6·3	0·11
	25	1·9*	6·2	0·11
	25	2·8*	6·7	0·01
	27	3·3*	6·7	0·004
	27	4·0*	6·5	0·02
Festuca	24	2·2*	6·5	0·005
	27	1·2*	6·8	0·002
Shrub-Dune	28	2·6†	6·9	0·01
	29	2·2†	6·8	0·01
	31	0·9†	7·0	0·02
	32	1·2†	6·9	0·02
Eucalyptus botryoides-Banksia integrifolia Associes	30	4·0	6·3	0·02
	32	2·9	6·6	0·02
	36	4·2	6·6	0·02
	50	5·5	6·1	0·03
Climax		Does not develop		

TABLE 3A.
Soil Properties on Transect at North Towrodgie.

——	W.R.C. (%).	Loss on Ignition (%).	pH.	Cl. (%).	Water Content (%). (14.7.38).
Spinifex	27	4·0*	6·5	0·03	3·3
Festuca (hummock) ..	24	2·2*	6·5	0·01	2·8
Shrub-dune	29	2·2†	6·8	0·01	0·7
Dune Forest	30	4·0	6·3	0·02	2·9

* Almost entirely due to calcium carbonate.
† Largely due to calcium carbonate.

(4). *Subsaline Lagoon Succession.*

This is a typical subsaline hydrosere, proceeding at the borders of the coastal lagoons whose formation by falling sea-level has been noted above. In general, forward succession in time seems to prevail, the allogenic causes of lagoon formation being too recent for any final equilibrium yet to have been reached. Retrogression by scouring is slight, and confined to the outer side of bends in the narrower parts of the lagoons, and especially at the lagoon mouths, where the outflow, though discontinuous, may sometimes be rapid (e.g., immediately following the breaking of the sand-bar obstruction after a period when outflow has been cut off).

In general, the lagoon borders are flat, and in some cases rise rather gradually to drier ground with alluvial soil carrying Mixed *Eucalyptus* Forest, regarded as the climax of the sere. The immediate cause of the succession is the raising of soil level by alluvium and plant remains, probably aided by fall in lagoon level;* the resultant fall in water-table relative to the soil surface allows a lowering of humus content (Table 4). The pH falls, as the buffering by lagoon waters decreases, to a minimum in the *Eucalyptus robusta* Associes, and rises again as the conditions become finally drier. Soil properties are listed in Table 4; over 50%, sometimes almost 100%, of the figures for loss on ignition represent humus. The properties of the first stage (*Phragmites*) are not listed, being atypical of this stage in other districts (infra); the properties for the *Cladium junceum* stage are bracketed, as this community is absent from the lagoon (Towrodgie Lagoon) where the other samples, representing a transect, were collected. The sample for the *Cladium junceum* stage represents part of the community beside Bellambi Lagoon, where the salinity and water-level were temporarily in a different state from Towrodgie Lagoon at the time of sampling.

The stages may be listed as follow:

TABLE 4.
Soil Properties for Subsaline Lagoon Succession.

——	W.R.C. (%).	Loss on Ignition (%).	pH.	Cl. (%).	Water Content (%). (4.7.38).
Juncus maritimus Associes ..	170	59	6·0	3·4	400
Cladium junceum Associes	(140)	(48)	(5·2)	(1·9)	(120)
Casuarina glauca Associes	140	50	4·6	2·8	220
Eucalyptus robusta Associes ..	140	47	3·4	0·45	33
Mixed *Eucalyptus* Forest (Climax)..	63–91	13–20	6·0–6·3	0·05–0·08	4–7
Melaleuca Communities:					
M. ericifolia, close to lagoon margin.	87	18	6·1	0·32	120
Melaleuca spp., several feet	39	6·9	5·7	0·02	12
above level of lagoon ..	35	8·8	5·8	0·12	12

* Over a long period of time. The outlet system causes a considerable fluctuation in lagoon level from season to season, but this fluctuation cancels out as a cause of succession.

(1). Phragmites communis *Associes.*

The half-submerged species *Phragmites communis* Trin. is not well developed in the lagoons studied, nor are the submerged or floating stages (*Zostèra nana, Ruppia maritima,* and filamentous algae such as *Cladophora*). The factor limiting the greater development of *Phragmites* appears to be the high and often rapidly-changing salinity. The species becomes more prominent in the upper waters of these lagoons, but here the neighbouring vegetation has been so much altered by clearing that a full study was unprofitable. In these upper reaches, where the salinity is low, *Triglochin procera, Alisma Plantago* and *Villarsia exaltata* F.v.M. occur occasionally, growing half-submerged.

In the parts of Towrodgie and Bellambi Lagoons where the succeeding stages (cf. Table 4) were most fully studied, there are local sparse stands of *Phragmites communis*; the soil (submerged) has here a low organic content and a pH approximating to the lagoon water. It includes a high proportion of intrusive dune sand. In other regions, the soil of the *Phragmites communis* Associes has typically a very high organic content, the pH approximating to that of the surrounding water, usually high.

(2). Juncus maritimus *Associes.*

Juncus maritimus is well developed around the margins of the lagoons studied (Pl. iv, C). The soil of this stage is always water-logged, though covered with surface water only when the lagoon level is abnormally high. The organic content is high; humus content lowers the pH below that of lagoon water. The chloride content is usually high.

(3). Cladium junceum *Associes.*

On the flatter parts of lagoon margins, a definite belt of *Cladium junceum* R.Br. develops behind the *Juncus maritimus* Associes. The soil has a lower water-content, organic content, and pH than the preceding stage.

The following herbaceous species occur among the dominants of stages (2) and (3), and occasionally on parts of the lagoon margin lacking *Cladium* and *Juncus*: *Salicornia australis, Spergularia rubra, Apium prostratum, Hydrocotyle vulgaris, Samolus repens, Dichondra repens, Wilsonia Backhousei, Lobelia anceps, Selliera radicans, Cotula coronopifolia, C. reptans.*

At the lagoon mouths, on flats of dune sand flooded by lagoon water, over which sea-water occasionally gains entry to the lagoons during rough weather, several of these species (e.g., *Apium prostratum, Hydrocotyle vulgaris*) often become temporarily established in what may be considered an intermediate between psammosere and hydrosere.

(4). Casuarina glauca *Associes.*

With decreasing water-content, soils of the lagoon margin carry a low forest of *Casuarina glauca.* Surface soils of this community are periodically, deeper soils continuously, water-logged. The pH, chloride content and organic content are slightly lower than in the preceding stages.

In addition to the dominant, *Casuarina glauca,* and the orchid, *Dendrobium teretifolium,* epiphytic on it, this stage possesses a ground layer of *Juncus maritimus* or *Cladium junceum,* together with some of the herbs of the preceding stages (e.g., *Selliera radicans*).

(5). Eucalyptus robusta *Associes.*

On drier soils, with somewhat reduced organic and chloride content, and with the lowest pH of the sere, a forest of *Eucalyptus robusta* develops, the trees being typically 40–50 feet in height. In typical parts of this stage, the ground layer is composed almost entirely of *Gahnia psittacorum*; occasionally, species relict from a previous stage (e.g., *Cladium junceum*) occur. In the dried parts of this associes, which may be regarded as an ecotone community, species of the climax community or of the *Melaleuca* Community (infra) enter.

(6). *Climax.*

With increasing efficiency of soil drainage, Mixed *Eucalyptus* Forest occurs. There is usually a rather abrupt rise in ground level of two feet or more between the preceding stage and this forest, which is interpreted as the climax. There seems little doubt, however, that the soil is alluvial, and has been a swamp soil in the past. The facts may be explained by a rather sudden fall in lagoon level at some past time, instead of a gradual increase in soil level by the accumulation of soil and plant remains. The occurrence of trees characteristic of damper stages (*Eucalyptus robusta, Melaleuca linariifolia*) at certain points within this forest does not appear to represent individual relics of an earlier stage as such; the time since the suggested fall in lagoon level would probably far exceed the life of any such tree. These trees may be regarded as relict species (not individuals), persisting where local conditions of drainage have remained in the earlier state.

The commonest trees of this forest are *Eucalyptus longifolia* and *E. punctata*; *E. botryoides*, *E. paniculata*, *E. eugenioides* and *E. pilularis* are also frequent. *E. robusta* occurs locally in damper situations, e.g., in slight depressions. The trees are rather widely spaced, and usually only some 50 feet in height. Old trees of *Melaleuca linariifolia*, up to 30 feet in height, are scattered throughout the forest. The lower layers are strongly suggestive of the mixed forest on tuffaceous mudstone discussed earlier. They include species of the normal *Eucalyptus pilularis* Association, species of the earlier stages of the lagoon sere, brush or brush ecotone species, and, much more rarely, dune forest species.

The lower strata have been too much altered by clearing to justify an estimate of the frequency of component species. Below is a list of species classified under life-forms, and exclusive of the trees mentioned above:

M: *Pittosporum undulatum, Breynia oblongifolia, Notelaea longifolia, Clerodendron tomentosum.*

M (climber): *Lyonsia straminea.*

N: *Persoonia linearis, P. salicina, Acacia juniperina, A. myrtifolia, A. suaveolens, Oxylobium trilobatum, Sida rhombifolia, Pimelea linifolia, Callistemon linearis, Leptospermum laevigatum, Melaleuca nodosa, Leucopogon Richei, Lantana camara* (introd.).

N (climbers): *Geitonoplesium cymosum, Stephania hernandifolia.*

Ch: *Viola hederacea, Halorrhagis teucrioides, Plantago lanceolata* (introd.).

H: *Cynodon dactylon, Eragrostis Brownii, Paspalum dilatatum* Poir. (introd.), *Sporobolus virginicus, Carex paniculata, Gahnia psittacorum, Juncus prismatocarpus, Rubus fruticosus* (introd.), *Oxalis corniculata, Dichondra repens.*

G: *Pteridium aquilinum, Cladium junceum, Burchardia umbellata.*

E: *Loranthus celastroides, Cassytha paniculata.*

S: *Opuntia inermis* P.DC. (introd.).

Th: *Solanum nigrum, Wahlenbergia gracilis, Hypochoeris glabra* (introd.), *Onopordon Acanthium* (introd.).

Soils of this climax forest have a greatly decreased water, chloride and organic content compared with the preceding stage. The pH is higher, due to drier conditions. The water-retaining capacity is moderately high.

In addition to the above communities, another, which may be termed the *Melaleuca* Community, is associated with the subsaline hydrosere. The species usually occur as a closed shrub thicket, sometimes due to regeneration after clearing. The following species frequently occur: *Melaleuca linariifolia, M. ericifolia, M. nodosa, Callistemon linearis*, while *M. styphelioides* and *M. thymifolia* are rare. The first species listed is fairly common as a low tree.

The *Melaleuca* Community may be regarded as a stage (alternative rather than regular) in the lagoon succession, immediately preceding the climax. It is found chiefly on flats subject to periodic flooding by rain-water, seldom on soils influenced by the more saline lagoon water.

Salinity of Soil Solution: The following figures, calculated on chloride and water contents of soils on July 4, 1938, indicate the salinity of the soil solution for that date:

Juncus maritimus Associes, 14°/oo; *Casuarina glauca* Associes, 21°/oo; *Eucalyptus robusta* Associes, 22°/oo; climax, 19–21°/oo.

It is apparent that compensation for decreased chloride content, by decreased moisture content, maintains the salinity of the soil solution fairly constant throughout the sere under these conditions; following wet weather, the discrepancy between the stages would increase. On this date, the salinity of Towrodgie Lagoon, on the borders of which the above samples were collected, was 17°/oo. At this time, Bellambi Lagoon (near mouth) had a salinity of 26°/oo (sea-water 35°/oo), and the *Cladium junceum* Associes, beside this part of Bellambi Lagoon, 26°/oo also.

The salinities of soil solutions for the *Melaleuca* communities listed in Table 4 are 4·3°/oo, 2·7°/oo and 16·2°/oo respectively. At the same time, part of this community was found bordering an isolated pool well above lagoon level; the salinity of this pool, whose water impregnated the soil of the *Melaleuca* Community, was only 1·2°/oo.

(5). *Sea-Cliff Vegetation.*

Zonation of communities on sea-cliffs in this region does not represent an autogenic succession any more than does the mosaic of developmental stages found on the Hawkesbury Sandstone scarp (Part ii of this series). Under present conditions, marine erosion renders any change retrogressive; however, any further fall in relative sea-level would probably promote conditions suitable for forward succession.

Two subclimax zones, dominated by herbs and shrubs respectively, lead back to the *Eucalyptus pilularis* Association. The first extends from a little above the extreme high-tide level to some 20–25 feet; the shrub community extends thence to the *Eucalyptus pilularis* Association, the distance varying from place to place, and being governed by the extent of unstable soil conditions on the cliff face and summit.

TABLE 5.

Soil Properties for Sea-Cliff Communities.

	W.R.C. (%).	Loss on Ignition (%).	pH.	Cl. (%).
Herb Zone (10–15 ft. above sea-level) ..	25	2·7	6·4	0·14
	27	3·9	7·4	0·01
	37	5·0	6·9	0·07
	37	6·2	7·2	0·02
Lowest part of Shrub Zone (25 ft. above sea-level).	59	7·7	7·0	0·10
Shrub Zone (30–50 ft. above sea-level) ..	45	20·0	6·6	0·09
	53	12·0	6·9	0·04
	60	14·0	5·3	0·13
	82	16·0	6·3	0·40

Properties of soils of these subclimax communities are listed in Table 5. The soils are derived from rocks of the Upper Coal Measures, and are usually, clayey, the lower samples with a greater or lesser admixture of beach sand. Chloride content appears to be governed by local factors of spray incidence and leaching, rather than by the height directly. The pH is usually high, probably because of the salts derived from sea spray. The limiting factor in shrub and tree development seems to be depth and stability of soil, rather than water-retaining capacity, humus or chloride content, pH, or wind exposure.

The herb zone contains the following species:

Ch: A, *Apium prostratum*, *Samolus repens*, *Lobelia anceps*; C, *Pelargonium australe*, *Plantago lanceolata* (introd.), *P. varia*; O (LC), *Scaevola calendulacea* Druce,* *Cotula coronopifolia*; O, *Tetragonia expansa*; R, *Rhagodia nutans*.

H: C, *Scirpus nodosus*, *Lomandra longifolia* Labill.; O, *Stenotaphrum secundatum* Kuntze (introd.).

Th: C, *Hypochoeris glabra* (introd.), *Sonchus oleraceus* (introd.); O, *Rumex crispus* (introd.), *Inula graveolens* (introd.); R, *Sonchus asper* Hill (introd.).

* Incorrectly listed in Part I as *Scaevola hispida*.

The species of the shrub zone which reaches the lowest level is *Westringia rosmariniformis*. Members of the herb zone which extend to the shrub zone are *Plantago* spp., *Scirpus nodosus, Lomandra longifolia, Stenotaphrum secundatum*, and all the therophytes listed above. In addition, the following species occur in the shrub zone (Pl. iv, D):

N: A, *Casuarina glauca* (bush; Pl. iv, E), *Banksia integrifolia* (bush), *Acacia myrtifolia, Leptospermum laevigatum, Westringia rosmariniformis*; C, *Pomaderris ferruginea* Sieb., *Lantana camara* (introd.); O, *Acacia suaveolens, Pultenaea retusa, Eucalyptus paniculata* (bush), *Melaleuca hypericifolia, Leucopogon Richei*; R, *Hakea pugioniformis, Persoonia salicina* (small-leaved variation), *Acacia juniperina, Oxylobium trilobatum, Zieria Smithii, Sida rhombifolia, Brachyloma daphnoides*; VR, *Pittosporum undulatum* (bush), *Breynia oblongifolia* (bush), *Phyllanthus Ferdinandi, Cupaniopsis anacardioides* Radlk. (bush), *Goodenia ovata, Olearia ramulosa* Benth.

N (climbers): A, *Kennedya rubicunda*; C, *Smilax glycyphylla, Hardenbergia monophylla*; O, *Clematis aristata, Billardiera scandens*; VR, *Stephania hernandifolia, Tylophora barbata.*

Ch: C, *Mesembryanthemum aequilaterale, Hibbertia Billardieri, H. volubilis*; O, *Commelina cyanea, Dianella revoluta, Glycine clandestina. Halorrhagis teucrioides*; R, *Scirpus cernuus* Vahl., *Bossiaea prostrata*; VR, *Desmodium varians.*

H: A, *Paspalum dilatatum* Poir. (introd.), *Rubus fruticosus* (introd.); C, *Themeda australis* Stapf., *Dichondra repens*; O(LC), *Gleichenia speluncae* R.Br.; R, *Cyperus polystachyus, Scirpus prolifer, Oxalis corniculata*; VR, *Adiantum aethiopicum.*

G: O, *Pteridium aquilinum*; R, *Lepidosperma laterale, Schoenus melanostachys, Tricoryne simplex.*

Th: O, *Phytolacca octandra* L. (introd.), *Taraxacum officinale* Weber (introd.); R, *Briza maxima* L. (introd.); *Poranthera microphylla, Anagallis arvensis* (introd.), *Polymeria calycina, Erythraea australis, Galium australe, Sherardia arvensis* (introd.), *Aster squamatus* (introd.), *Bidens pilosus, Onopordon Acanthium* (introd.), *Sonchus megalocarpus* J. M. Black (introd.).

E: O(LC), *Cassytha paniculata.*

The above list testifies in itself to the diversity of habitats at this level on the sea-cliffs. The species include normal units of the *Eucalyptus pilularis* Association (e.g., *Eucalyptus paniculata, Kennedya rubicunda, Oxylobium trilobatum*); brush types confined to relatively moist and sheltered parts of the cliffs (*Pittosporum undulatum, Tylophora barbata, Stephania hernandifolia, Adiantum aethiopicum*); swamp types confined to local soaks (*Cyperus melanostachys, Lepidosperma laterale, Scirpus prolifer*); and members of the coastal psammosere (*Banksia integrifolia, Leptospermum laevigatum, Mesembryanthemum aequilaterale*) and lagoon succession (*Apium prostratum, Lobelia anceps, Cotula coronopifolia*).

The sea-cliff vegetation bears some resemblance to the vegetation of the Five Islands (Davis, Day and Waterhouse, 1938). Of the Five Islands species, some 50% are represented on the sea-cliffs studied, and some 70% on the sea-cliffs, dunes and lagoon sere taken together.

The development of the *Eucalyptus pilularis* Association, on cliff tops with deeper and more stable soil, represents an increase in the height of *Banksia integrifolia* and *Eucalyptus paniculata*, and addition of *E. pilularis* and *Syncarpia laurifolia* Ten. *Banksia integrifolia* does not extend inland more than some 50 yards in this region; some species of the lower strata of the sea-cliff vegetation (e.g., *Leptospermum laevigatum*) are even more closely restricted to the immediate vicinity of the sea. *Casuarina glauca*, which occurs as stunted bushes in the shrub zone on the cliffs, very seldom reaches tree status; as soon as conditions become suitable for tree development, some factor (probably competition) excludes this species.

Note: In this and the preceding part (Davis, 1941), species have been classified into life-forms as closely as possible. Strict classification is often difficult because of the lack of a definitely unfavourable season (cf. Part i, Climate). Some species are listed as of different life-form in different communities; thus a cryptophyte is classed as G in a dry community, HH where it extends into a swamp community; or a typical cryptophyte, if growing in a situation of restricted soil depth (e.g., on the Hawkesbury Sandstone scarp) becomes a hemicryptophyte. Climbers have been referred to the class of phanerophytes whose height they reach most typically in the community concerned;

in some cases, a climbing plant is classed as a chamaephyte if it occurs in a certain community typically as a straggling plant less than one foot in height. In the case of phanerophytes (including climbers), if any doubt exists as to which height-class a species most characteristically falls into, in the community concerned, it is classed in the upper of the two possible classes. The rooted hemiparasite *Cassytha* is classed throughout as an epiphyte.

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EXPLANATION OF PLATES III-IV.

Plate iii.

A.—Pioneer stages of the psammosere at Towrodgie. *Festuca litoralis* holds the sand in hummocks where the surrounding sand has been removed by wind action; stolons of *Spinifex hirsutus* colonize the sand at the new level.

B.—Psammosere at Towrodgie: *Spinifex hirsutus* and tussocks of *Festuca litoralis* to the left; shrub stage on crest of dune; dune forest (lower strata cleared) on inshore slope.

C.—Pioneer stages of psammosere (*Spinifex, Festuca*) in equilibrium with marine erosion at the extreme limit of wave action, Towrodgie Beach. Shrub dune in background, blow-out area almost devoid of vegetation in left middle-distance.

D.—Dune forest and shrubs on residual hillock at Bellambi, the surrounding area having been denuded by wind action. The foreground consists of pioneer dune plants, soil and vegetation being slightly atypical of this stage, due to occasional flooding by lagoon water.

E.—Panorama of mouth of Bellambi Lagoon, north bank. Both hydrosere and psammosere are affected by scouring caused by occasional rapid outflow of pent-up lagoon waters.

Plate iv.

A.—*Eucalyptus pilularis* Association near Austinmer.

B.—Mixed *Eucalyptus* Forest on tuffaceous mudstone, north of Towrodgie Creek. The lower strata have been altered by clearing.

C.—Early stages of lagoon succession, Towrodgie: *Juncus maritimus* Associes backed by *Casuarina glauca* Associes. Open waters of lagoon on extreme right; *Phragmites communis* Associes scarcely developed.

D.—Sea-cliff at North Austinmer, with shrub zone on upper parts.

E.—Shrub zone on sea-cliff, South Austinmer: Stunted form of *Casuarina glauca*. The camera case is 8 inches high.

Appendix.

Life-Form Spectra for Communities of Coastal Slopes and Plain.

	MM.	M.	N.	Ch.	H.	G.	HH.	Th.	S.	E.	No. of Species.
Eucalyptus pilularis Association	7	6	26 (22+4)	15	19	11	..	13	..	3	109
Brush (excluding purely ecotone species).	53 (41+12)	15 (8+7)	3	..	13	3	..	..	..	13	96
Climax to Lagoon Sere (Mixed *Eucalyptus* Forest).	14	10 (8+2)	30 (26+4)	6	20	6	..	8	2	4	50

Conventional lettering for life-forms.

Where classes MM, M and/or N are represented by climbers in addition to other forms, the percentages of climbers are also indicated (second of two numbers in brackets below percentage of total).